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A CASE OF ABNORMALITY IN CATS' PAWS.

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THIS paper contains an account of facts learned by the study of the walking pads, the muscular, vascular, nervous, and skeletal systems of the manus of a polydactyle and syndactyle cat. The cat furnishing the material for this study was one of a strain of polydactyle cats living in Cambridge, Massachusetts, and descended from a polydactyle cat which lived at the astronomical observatory of Harvard University. All four legs of the cat dissected were preserved in alcohol and were kindly given me for study by Dr. C. B. Davenport, under whose direction the work was done. To him and to Prof. E. L. Mark I wish to extend my thanks for kind advice and criticism.

Each fore paw had six toes; the toes of the hind paws were fused in pairs almost to the ends of the claws, as is shown in Figs. 1 and 2.

The syndactyle hind paws have not been dissected, but a drawing of the palmar and dorsal surfaces is shown in Figs. 1 and 2 respectively. Walking pads and distal phalanges both indicate that the four digits are fused in pairs.

I wished to determine, if possible, which toe of each fore paw is the extra one, and what is the nature of the evidence.

I have been unable to learn of any account of a study on material precisely similar to this. The collection of facts in Bateson's "Materials for the Study of Variation" covers the ground worked over by previous authors, and this, with Poulton's papers, includes an account of all the published facts on the subject, as far as known to me. Previous study has been



FIG. 1.

FIG. 1. — Palmar aspect of hind paw of abnormal cat, showing fused pads.



FIG. 2.

FIG. 2. — Dorsal aspect of hind paw of abnormal cat, showing claws fused in pairs.

only on the walking pads and on the skeleton. Bateson described principally skeletal structures, and Poulton studied the walking pads. They have drawn their conclusions as to the true nature of polydactylism from facts learned from these two organs only. It is, of course, desirable to have as complete a knowledge as possible of the anatomy of the

paw, as a basis for any conclusions to be drawn. I find from my dissections that the evidence furnished by the walking pads and skeletal system is borne out by the other organs mentioned.

The general appearance of the polydactyle paw studied, apart from the increased number of digits, is quite different from that of a normal fore paw. The radial digit in the polydactyle paw extended much nearer to the end of the paw than the pollex normally does, the digits being more nearly of the same length than in the normal paw. A comparison of the relative positions of the ungual and middle phalanges during the retraction of the former will be made when we come to the study of the bones.

The walking pads of the polydactyle paw (Fig. 4) differ from those of the normal paw (Fig. 3) in that the phalango-metacarpal

pad (*pulv.phlx-mt'carp.*) of the polydactyle is five-lobed instead of three-lobed as normally, and the lobes in the polydactyle paw are more clearly marked off from one another than in the normal paw. The parts of the five-lobed pad which appear to correspond to the phalango-metacarpal pad of the normal paw are the three external lobes which are more closely associated with one another than with the two internal lobes; while the two internal lobes are more closely applied to each other than to the three external ones. That

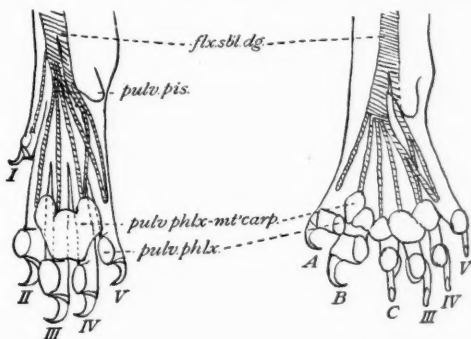


FIG. 3.

FIG. 4.

FIG. 3. — Palmar aspect of right fore paw of normal cat.

FIG. 4. — Palmar aspect of right fore paw of polydactyle cat. *A*, radial digit; *B*, second digit, etc.; *I*, pollex; *II*, index; *III*, medius; *IV*, annulus; *V*, minimus; *flx.sbl.dg.*, flexor sublimis digitorum; *pulv.phlx.*, phalangeal pads; *pulv.phlx-mt'carp.*, phalango-metacarpal pad; *pulv.pis.*, pisiform pad.

five lobes instead of three existed in the polydactyle paw is probably due to the fact that one lobe was added by the formation of an extra digit, and that the growth of the radial digit, which occurred to so unusual an extent that it functioned more like a walking digit than the pollex normally does, excited the growth of a phalango-metacarpal pad on this digit also. In both the normal and the polydactyle paw there is a walking pad on the distal end of each middle phalanx (*pulv.phlx.*) and on the pisiform bone (*pulv.pis.*).

MUSCLES.

As in the normal fore paw, the muscles *extensor carpi radialis longior* and *extensor carpi radialis brevior* (Figs. 5, 6, *ext.carp.r.lg.* and *ext.carp.r.br.*) are inserted on the proximal dorsal surface of the second and third (counting from the radial side) metacarpal bones respectively.

Considering the evidence of these two muscles alone, we should infer that in the polydactyle paw the radial side is normally formed and that the extra digit is external to (on the

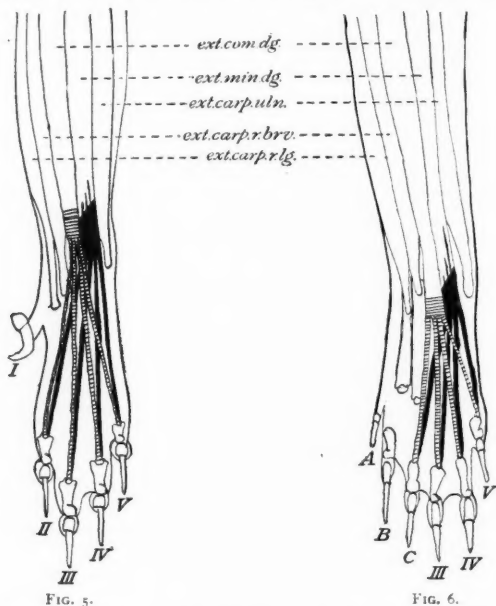


FIG. 5.—Dorsal aspect of left manus of normal cat, showing dissection of muscles. *ext.carp.r.br.*, extensor carpi radialis brevior; *ext.carp.r.lg.*, extensor carpi radialis longior; *ext.carp.uln.*, extensor carpi ulnaris; *ext.com.dg.*, extensor communis digitorum; *ext.min.dg.*, extensor minimi digiti.

FIG. 6.—Dorsal aspect of left manus of polydactyle cat, showing dissections of same muscles as in Fig. 5.

ulnar side of) the third one, for in the polydactyle paw there are three digits external to the insertion of the *extensor carpi radialis brevior*, whereas in the normal paw there are only

two. Such an inference, however, is not borne out by the evidence of other muscles and tissues.

Muscles *extensor communis digitorum* and *extensor minimi digiti* (Figs. 5, 6, *ext.com.dg.* and *ext.min.dg.*) in both normal

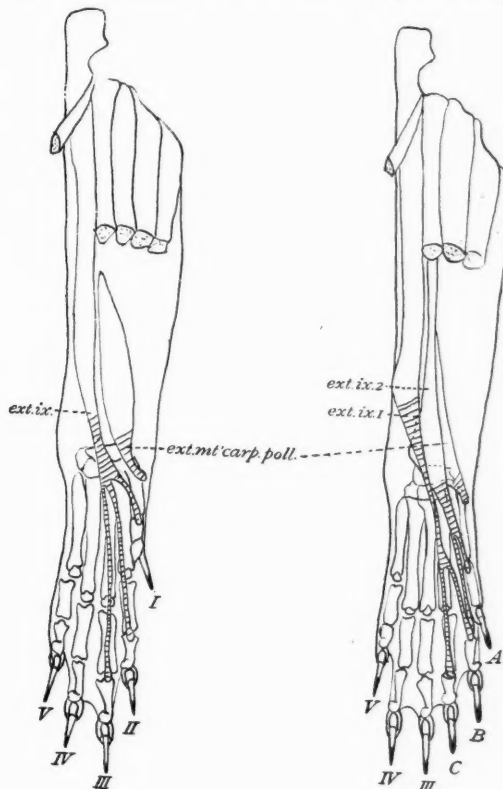


FIG. 7.

FIG. 8.

FIG. 7. — Dorsal aspect of right manus of normal cat, showing dissection of deep muscles. *ext.ix.*, extensor indicis; *ext.mt'carp. poll.*, extensor metacarpi pollicis.

FIG. 8. — Dorsal aspect of right manus of polydactyle cat, showing same deep muscles as in Fig. 7. (See text for description of *ext.ix.1* and *ext.ix.2*.)

and polydactyle paw extend to the proximal dorsal surface of the middle phalanx of each of the four external digits. The distribution of these muscles points to the inference that the

four external digits of the polydactyle paw correspond to the external four in the normal cat, and that the extra digit occurs on the radial side of the four external digits, an inference which, with some modifications, seems to be confirmed by other facts.

Muscle *extensor carpi ulnaris* (Figs. 5, 6, *ext.carp.uln.*) in both normal and polydactyle paw is inserted on the ulnar metacarpal.

The *indicator* (Fig. 7, *ext.ix.*) is somewhat variable in respect to its insertion, even in normal specimens, sometimes supplying the pollex, index, and medius, sometimes only the pollex and index. In the polydactyle paw a peculiar arrangement exists, in that there are two muscles in place of one. That which, from relative position and insertion, seems to correspond to the normal one (Fig. 8, *ext.ix.1*) is distributed to the second (*B*) and third (*C*) digits.

In addition to this muscle there is under it, and distinct from it, another muscle (*ext.ix.2*), which passes in the same general direction to the two internal digits (*A* and *B*, Fig. 8). This muscle has a more distal origin than does the one supplying digits *B* and *C*; it originates from the dorsal border of the ulna and passes directly over the muscle *extensor metacarpi pollicis* (*ext.mt'carp.poll.*). Comparisons of the two indicators with each other and with the normal muscle seem to point to a readjustment to meet a new condition of the manus.

In both the normal and the polydactyle manus the radial metacarpal furnishes insertion for the *extensor metacarpi pollicis* (Figs. 7, 8, *ext.mt'carp.poll.*).

Muscle *flexor carpi radialis* in both the normal and the polydactyle paw has its tendons inserted on the proximal ends of the palmar surface of the second (counting from the radial side) metacarpal.

The ulnar part of the *flexor sublimis digitorum* in both normal and polydactyle paws has tendons extending to the first and second digits, counting from the ulnar side (Figs. 3, 4, *flx.sb'l.dg.*), while the tendons from the radial part of the muscle extend in the normal paw to the four, and in the polydactyle paw to the five, digits nearest to the radial side.

The fact that in the polydactyle paw the union between the tendons to the digits marked *IV* and *V* (Fig. 4) extends further distally than in the normal paw (Fig. 3) is apparently less important than the fact that in the polydactyle paw the radial part of the muscle has five tendons while the normal paw has only four.

Muscle *flexor profundus digitorum* (Figs. 9, 10, *flx. profnd. dg.*) has in the normal paw five, and in the hexadactyle paw six,

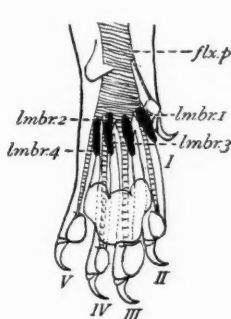


FIG. 9.



FIG. 10.

FIG. 9. — Palmar aspect of left manus of normal cat, showing dissection of deep muscles.

FIG. 10. — Palmar aspect of left manus of polydactyle cat, showing muscles as in Fig. 9. *A*, radial digit of polydactyle manus; *I*, that of normal manus; *flx. profnd. dg.*, flexor profundus digitorum; *lmbr. 1-4*, lumbricales 1-4.

tendons distributed one to each digit. There is no evidence here as to which digit is the extra one.

Muscle *flexor carpi ulnaris* is inserted on the pisiform bone in both normal and polydactyle paws.

There are four *lumbricales* in both normal and polydactyle paws (Figs. 9, 10, *lmbr. 1-4*). In both cases these are inserted one each on the radial side of the proximal phalanx of each of the four external digits. In the polydactyle paw there is no lumbrical superficial to the radial border of the distal part of the *flexor profundus digitorum*.

BLOOD VESSELS.

The arrangement of the veins on the dorsal surface of the normal and the polydactyle fore paw is shown in Figs. 11 and 12. The only points that can be taken as homologous for determining the corresponding veins in the normal and polydactyle paw are the most distal point of the loop formed by the anastomosis of the ulnar (*v.uln.*) with the radial (*v.r.*) vein. This point in both normal and polydactyle paws seems to be between



FIG. 11.

FIG. 11. — Dorsal aspect of left manus of normal cat, showing arrangement of veins. *v.uln.*, ulnar vein; *v.r.*, radial vein.

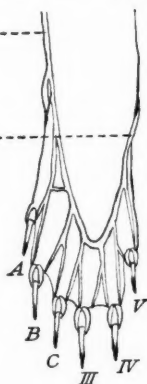


FIG. 12.

FIG. 12. — Dorsal aspect of left manus of polydactyle cat, showing arrangement of veins.

digits marked *III* and *IV*. Starting from this point, we see that in the normal paw there are three branches, and in the polydactyle paw four branches, which contribute to the radial vein. These facts suggest the conclusion that the extra digit of the polydactyle paw is on the radial side; but owing to the uncertainty of the exact position of this point of reference, the evidence from the veins

is of less value than that from some of the other organs.

In studying the arteries the only fact which throws any light on the problem is the relative size of the digital branches from the *palmar arch* (Figs. 13, 14). The branch which supplies the radial digit is small in both the normal and the polydactyle paw. In the normal paw the branch to the index is as large as the branches to each of the other three digits; but in the polydactyle paw the branches to digits *A + B* and *B + C* (Fig. 14), while about equal to each other in size, are much smaller than those to the external digits.

NERVES

The *radial nerve* after becoming subcutaneous follows the course and distribution of the dorsal veins, which are shown in Figs. 11 and 12. The *median nerve* (Figs. 15, 16, *n.m.*) besides supplying the muscle *flexor communis digitorum* is distributed to *four* consecutive digits, beginning with the radial side, in the normal and to *five* consecutive digits in the polydactyle paw. In the normal manus the *ulnar nerve* divides, just below the olecranon, into an inner (ventral, *n.uln.v.*) and an outer (dorsal, *n.uln.d.*) branch (Fig. 15). The outer (dorsal) branch passes to the outer side of digit *V* and also sends dorsally a branch to the internal side of the same digit and to the external side of digit *IV*. In both normal and polydactyle manus the internal (ventral) branch of the ulnar (Figs. 15, 16, *n.uln.v.*) supplies the three external digits.

For a point of reference in comparing the nerves we may take a small branch which passes from the *ulnar* to the *median* nerve. This unites with that branch of the median which in the normal manus (Fig. 15) passes to the ulnar side of digit *III* and to the radial side of digit *IV*. In the *hexadactyle manus* (Fig. 16) the branch of the median nerve which is joined by the ulnar nerve likewise passes to the ulnar side of digit *III* and to the radial side of digit *IV*. There is, then, in the abnormal manus radially to the nerve of reference one more digit than exists in the normal manus. This makes it apparent that the modification producing polydactylism has occurred on the radial side of the manus.

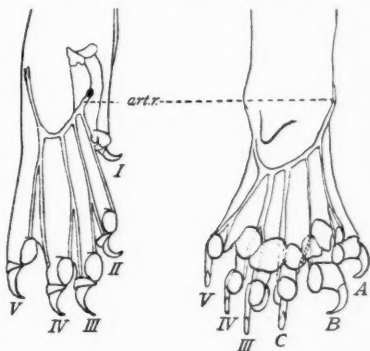


FIG. 13.

FIG. 14.

FIG. 13. — Palmar aspect of left manus of normal cat.
art.x., radial artery.

FIG. 14. — Palmar aspect of left manus of polydactyle cat.

SKELETON.

The ulnar, radial, and carpal bones are practically the same in number, relative size, shape, proportion, etc., in the normal and abnormal manus. There are in the polydactyle paw six *metacarpals*, a pollex of two phalanges, and five digits, each with three phalanges. All the bones of the normal paw (Fig. 17) are larger and stouter than those of the polydactyle paw (Fig. 18). Bones of a normal paw were prepared for the purpose of making comparisons with the abnormal skeleton in respect to weight, relative proportions, etc. In making these comparisons, allowances are made for the general differences mentioned above.

The *radial sesamoid* of the *carpus* of the six-toed cat (*ses.*, Fig. 18) is fused to the radial side

of the scapho-lunar (*scph-lun.*) and furnishes the place of articulation for the metacarpal of the pollex. In the polydactyle manus the four external metacarpals (*mt' carp.*) have the same articulations with the distal row of carpals as in the normal manus. In the normal manus the *pollex* articulates with the *trapezium* (*trs.*), while in the abnormal manus (Fig. 18) the

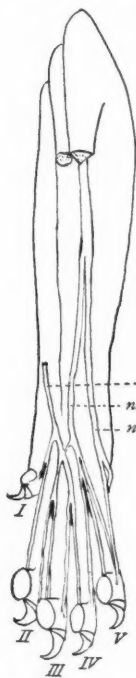


FIG. 15.

FIG. 15. — Palmar aspect of right manus of normal cat. *n.m.*, median nerve; *n.uln.d.*, dorsal branch of ulnar nerve; *n.uln.v.*, ventral branch of ulnar nerve.

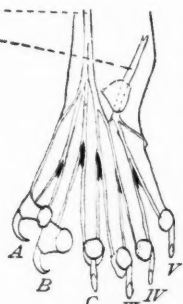


FIG. 16.

FIG. 16. — Palmar aspect of right manus of polydactyle cat.

metacarpal of digit *B* articulates with the trapezium. Metacarpal of digit *A* (Fig. 18) articulates, as previously stated, with the radial sesamoid (*ses.*), which is fused to the scapho-lunar (*scph-lun.*).

The metacarpal bones in both manus are similar, except that there is in the abnormal manus no "groove" for the radial

artery. The metacarpals, as well as the other bones of the pollices, vary considerably in length and thickness, and in this respect will be considered more closely later.

There is no particularly noticeable variation in the proximal series of phalanges (*phlx.prx.*). These bones have the least distinctive characters, differing from one another chiefly in size.

The series of middle phalanges (*phlx.m.*) furnishes very interesting conditions. In both the normal and abnormal manus the three external (ulnar) middle phalanges are carved away on the ulnar side to allow for the retraction of the corresponding ungual phalanges (*phlx.ung.*). The middle phalanx

of the index of the normal manus is likewise carved away on the ulnar side, but in the abnormal manus the digit (*C*, Fig. 18) next to the three ulnar digits is carved away on neither side and is therefore "indifferent." The middle phalanx of digit *B* (Fig. 18) has no counterpart in the normal

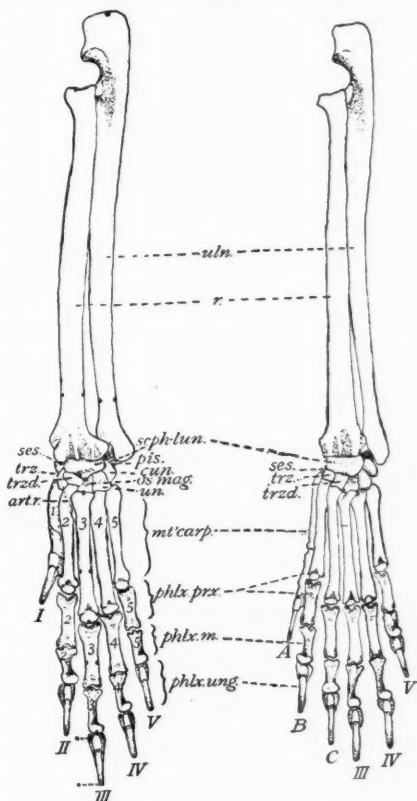


FIG. 17.

FIG. 18.

FIG. 17. — Dorsal aspect of skeleton of left manus of normal cat.

FIG. 18. — Dorsal aspect of left manus of hexadactyle cat. *A*, radial digit of abnormal manus; *I*, that of normal manus; *art.r.*, groove for radial artery; *cun.*, cuneiform; *mt'carp.*, metacarpals; *un.*, uncinate; *os mag.*, os magnum; *phlx.m.*, middle phalanges; *phlx.prx.*, proximal phalanges; *phlx.ung.*, ungual phalanges; *pis.*, pisiform; *r.*, radius; *scph-lun.*, scapho-lunar; *ses.*, sesamoid; *trz.*, trapezium; *trzd.*, trapezoid; *uln.*, ulna.

manus, except that it is somewhat like a pollex, which, when retractable, as occasionally happens, is carved away on the radial side.

The ungual phalanges are too nearly alike in the normal and the polydactyle paw to be of service as far as our purpose is concerned.

GENERAL CONSIDERATIONS.

The facts learned from the dissection of the polydactyle manus are in part contradictory; that is, some facts suggest that the extra digit occurs on the radial side of the paw, whereas others indicate an extra digit on the ulnar side; but, on the whole, the balance of the evidence points to the existence of the extra digit on the radial side of the three ulnar digits. The evidence which the bones furnish seems to be the most satisfactory, and is borne out in the majority of cases by the other tissues. The middle phalanges of digits *III*, *IV*, and *V* (Figs. 17, 18) are carved away on the ulnar side, as normally. The middle phalanx of digit *C* (Fig. 18) is an indifferent digit, *i.e.*, carved away on neither side. In this it more resembles a pollex than a digit. The middle phalanx of digit *B* (Fig. 18) is carved away on the radial side, in this respect resembling a pollex more than a digit. Digits *III*, *IV*, and *V* in both manus are distinctly similar. Regarding the articulation of the metacarpals with the carpals, it is seen that the five external digits of the abnormal manus have the same articulation as do the five digits of the normal manus. The pollex of the abnormal manus has the articulation abnormal, in that it is with the radial sesamoid, which in this case is fused with the scapho-lunar. Here the five digits nearest the ulnar side are normal.

Considering the three ulnar digits of the abnormal manus to correspond to normal digits, one is naturally led to inquire what modifications the manus has undergone that there should be three digits instead of two on the radial side of the three ulnar normal ones. Further evidence from the bones is interesting in respect to this query.

A comparison of the indices and the weights of the individual bones of both the normal and abnormal manus is shown in the accompanying table. For the purpose of more accurate comparison of the two sets of bones, I have figured the percentage which each bone bears to the total weight of all the bones of the manus to which it belongs (including ulna and radius). The indices of the bones were obtained by finding the ratio between the minimum thickness and the maximum length of each bone. The actual points of measurement are shown by the dots in Fig. 17, *III*. Inspection of the bones first leads us to see that digit *A* (Fig. 18) is much longer than the normal pollex and presents in the undissected manus more the character of a finger than of a pollex. The bones, however, are distinctly those of a pollex, since there are two phalanges only; but they are longer and more slender. In this respect they resemble a finger. The bones of digit *B* (Fig. 18) are more like a pollex than are those of the digit which normally adjoins the pollex. One can also see that digit *C* (Fig. 18) is more like a pollex than is the digit which is normally fourth from the ulnar side. What further facts are there to bear out the idea that where there are normally two digits, there abnormally occur three, each of which partakes somewhat of the general characters of the others?

It is a fact that where normally two digits are found, namely, a pollex and an index, there are found in this special case three, and that the material which would normally form two digits has so distributed itself that each of the three digits which actually occurs partakes of the nature of the other two. Is the abnormal pollex two-thirds pollex and one-third index; the digit next the pollex, one-half index and one-half pollex; and the digit *C* (Fig. 18) two-thirds index and one-third pollex? There seems to be some relation of this sort.

If we compare the indices and the relative weights of the two manus, we come to a like conclusion (see accompanying table). For example, comparing the percentages of total *weights* in the abnormal manus, metacarpal *A* (Fig. 18) is more like the other metacarpals of its manus than is metacarpal *I* of the normal manus like the other metacarpals of its manus;

NORMAL.

	GRAMS WEIGHT.	PERCENTAGE WEIGHT.	MILLIMETERS MEASUREMENT.	PERCENTAGE INDEX.
Ulna	3.467	.333	45 × 1030	.0437
Radius	2.679	.257	52 × 878	.0592
Carpals699	.067	—	—
Metacarpals				
I135	.012	32 × 112	.286
II423	.040	28 × 284	.0986
III525	.054	32 × 321	.0997
IV445	.043	30 × 300	.100
V348	.033	28 × 247	.113
Totals of metacarpals .	1.876	.182	—	—
Proximal phalanges				
I096	.0092	32 × 82	.402
II157	.0158	32 × 136	.235
III188	.0187	33 × 155	.203
IV161	.0154	30 × 147	.204
V127	.0122	29 × 118	.245
Totals of proximal phalanges .	.729	.0713	—	—
Middle phalanges				
I	—	—	—	—
II097	.0093	23 × 94	.244
III108	.0103	23 × 115	.200
IV094	.0090	23 × 108	.213
V078	.0075	28 × 82	.341
Totals of middle phalanges .	.377	.0361	—	—
Distal phalanges				
I150	.0144	34 × 102	.333
II116	.0111	30 × 100	.300
III125	.0120	28 × 100	.280
IV102	.0098	28 × 101	.278
V089	.0086	28 × 93	.301
Totals of distal phalanges .	.582	.0559	—	—
Total of all bones . .	11.030	—	—	—

POLYDACTYLE.

	GRAMS WEIGHT.	PERCENTAGE WEIGHT.	MILLIMETERS MEASUREMENT.	PERCENTAGE INDEX.
Ulna	2.829	.330	40 × 1015	.0394
Radius	2.188	.255	42 × 850	.0490
Carpals529	.061	—	—
Metacarpals				
A097	.011	20 × 157	.127
B261	.030	27 × 231	.113
C295	.034	26 × 260	.100
III292	.034	26 × 278	.094
IV291	.034	24 × 260	.091
V237	.027	25 × 212	.118
Totals of metacarpals .	1.473	.170	—	—
Proximal phalanges				
A054	.0063	19 × 103	.184
B123	.0144	31 × 120	.258
C123	.0144	30 × 126	.238
III133	.0166	28 × 140	.200
IV123	.0144	27 × 132	.204
V090	.0105	28 × 101	.277
Totals of proximal phalanges646	.0766	—	—
Middle phalanges				
A	—	—	—	—
B073	.0085	25 × 85	.294
C071	.0083	23 × 83	.277
III078	.0091	18 × 101	.178
IV073	.0085	20 × 96	.208
V057	.0066	27 × 72	.375
Totals of middle phalanges352	.0410	—	—
Distal phalanges				
A092	.0107	24 × 79	.304
B110	.0128	25 × 99	.252
C105	.0123	28 × 102	.274
III096	.0112	28 × 99	.282
IV080	.0093	26 × 94	.276
V069	.0080	27 × 89	.315
Totals of distal phalanges552	.0643	—	—
Total of all bones	8.569	—	—	—

likewise, the metacarpal of digit *B* is more like metacarpal *A* than the metacarpal of digit *II* of the normal manus is like its pollex. Again, the metacarpal of digit *C* is more like its pollex metacarpal *A* than is the metacarpal of digit *III* of the normal manus like its pollex.

The same fact is also borne out by the comparison of the *indices*, which are mathematical expressions of the forms of the bones and can, therefore, be combined in the same way as the percentage weights.

That the two normal radial digits have given place to three, each of which partakes somewhat of the nature of the others, is shown by a consideration of the tissue systems, and in no way does this explanation meet with a decided contradiction. The evidence of the dorsal veins is negative and not contradictory.

I know of no case of polydactylism similar to the one here described. One which is somewhat similar is described by Windle (*Journ. of Anat.*, Vol. XXVI, 1891, p. 100), who in conclusion says: "The musculature shows that where there is an additional digit on the radial side, it and the digit next to the index both partake of the nature of thumbs and may be looked upon as the first and second digits of a hexadactylous manus."

In the case described in this paper, there is no reversion, and the anatomy of the polydactyle paw, as here worked out, has no bearing on either the "pre-pollex" or the "post-minimus" theories. The abnormality seems to result purely from a readjustment of parts. The only definite statement which can be made in regard to this case is that where normally two digits occur, three have here appeared, and that each of these three partakes more of the nature of the others than one of the two normal digits does of the other.

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THE GASTRULATION OF THE EGG OF BUFO LENTIGINOSUS.

HELEN DEAN KING.

AN examination of the literature dealing with the early development of the amphibian egg shows many conflicting observations and theories regarding the origin of the blastopore and the manner of formation of the mesoderm and notochord. It is evident, therefore, that more forms must be studied and the observations in some cases carefully repeated before any general conclusions regarding the origin of these structures can be drawn for the entire group.

The amphibian eggs that have been most studied are those of *Rana*, *Triton*, *Axolotl*, and *Bombinator*. The present paper deals with the early development of the egg of *Bufo lentiginosus* from the end of cleavage until the closure of the blastopore. The eggs of this amphibian, although very abundant and easily obtained, have been but little used either for observation or for experiment, owing, doubtless, to their small size and to their relatively deep pigmentation, which makes it very difficult to follow the fate of living cells.

METHOD.

In preparation for sectioning, eggs were killed in various fluids: picro-acetic, picro-sulphuric, formalin, and corrosive-acetic. By far the best results were obtained with corrosive-acetic (5 per cent acetic). Formalin (3-10 per cent) gives exceedingly good preparations for a study of surface structures, but it cannot be relied on to give histological details, as it usually produces numerous cracks in various parts of the egg. The sections were stained on the slide with the mixture of borax carmine and Lyon's blue, recommended in a previous paper (King, 10). With the use of this stain the

nuclei appear red, the yolk blue, and the cell outlines are brought out with great clearness.

THE FORMATION OF THE BLASTOPORE.

The egg of *Bufo lentiginosus* probably contains a greater amount of pigment in proportion to its size than that of any other common amphibian. It is, therefore, very difficult to study the movements of individual cells before and during the formation of the blastopore, as has been done to some extent in the eggs of several other species of amphibians, where the pigmentation is less extensive and cell outlines can be readily determined.

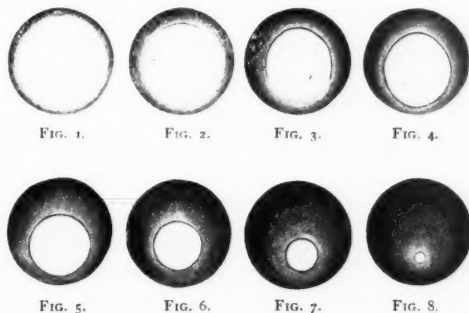
In the egg of *Bufo* the pigmentation extends in all cases some distance below the equator, and I have frequently found eggs in which fully three-fourths of the surface was deeply pigmented before the appearance of the blastopore. Individual eggs, even from the same female, differ greatly in the amount of pigment they contain. As a rule, the pigment line extends farther down on one side of the egg than on the other, as seen in Fig. 1, agreeing in this respect with the frog's egg according to Schultze (24), Morgan and Tsuda (17), and Wilson (27).

Sections through an egg at the close of the blastula stage show a large segmentation cavity in the upper hemisphere. Its dorsal wall is formed, as in the frog, of three or four layers of small angular cells of uniform size. The cells forming the outer surface of the egg are almost completely filled with pigment granules, and a considerable amount of pigment is scattered throughout all the cells of the upper part of the egg. The yolk cells below the segmentation cavity are much larger, more rounded, and stain less intensely than the cells in the upper hemisphere. There is the same gradual increase in the size of the cells from the upper to the lower pole that other investigators have noted in the frog's egg.

The dorsal lip of the blastopore invariably appears some distance below the equator of the egg, but never in the middle of the lower hemisphere, as maintained by Houssay (8) for the axolotl and Jordan (9) for the newt.

If the egg has but the usual amount of pigment, the first evidence of the blastopore, in surface view, is a short, dark, almost straight line at the extreme edge of the black cells (Fig. 1). If the pigmentation is unusually extensive, the blastopore appears in its same relative position with respect to the lower pole of the egg but distinctly within the black cells. Whether there is, as the first step in the formation of the blastopore, a "lining up" of the ectoderm cells, as described by Wilson for the frog, I have not been able to determine.

Sections of an egg at the beginning of gastrulation show that the dorsal lip of the blastopore is formed primarily by a sinking in of several of the surface cells (Fig. 9). The shallow



FIGS. 1-8. — Surface views of the lower hemisphere of an egg during the formation and closure of the blastopore.

depression thus formed is rapidly extended and soon becomes a pronounced furrow (Fig. 10). The cells involved in this sinking in are all, without question, large yolk cells which are decidedly wedge-shaped and contain a considerable amount of pigment in their smaller ends turned towards the exterior (Figs. 9, 10, 11).

After the lateral extension of the dorsal lip to form a crescent, a sagittal section through the blastopore shows that the furrow has deepened considerably and that its inner end is turned up towards the dark pole (Fig. 11). From this time on there is a marked difference in appearance between the cells forming the dorsal wall of the archenteron and those forming the ventral wall. The cells of the dorsal wall are small, angular,

deeply pigmented cells, and they are apparently exactly like the small cells forming the upper surface of the egg, except that they do not contain quite as much pigment. The yolk cells which form the floor of the archenteron are three or four times larger than the cells of the dorsal wall, and they

are more rounded and contain little if any pigment. The distinction between these cells is made more evident by the fact that with the combination stain used all the yolk cells appear decidedly blue, while the cells of the dorsal wall of the archenteron and, in fact, all the cells of the upper hemisphere, take a distinctly reddish tint. The cells at the anterior end of the archenteron are still wedge-shaped at this stage. They are intermediate in size between the cells forming the dorsal wall and those forming the ventral wall of the archenteron, and they stain like the yolk cells.

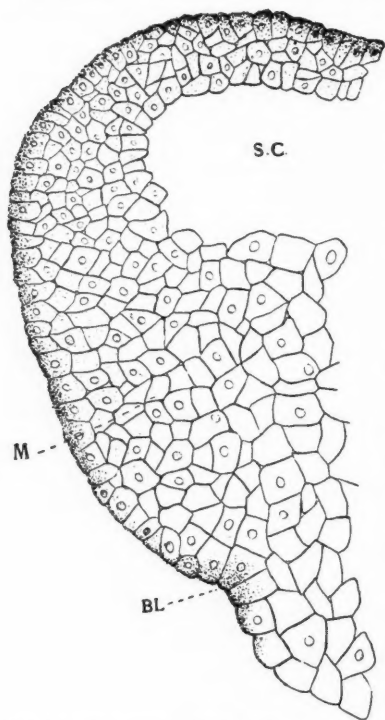


FIG. 9.—Part of a section through the median plane of the blastopore at the stage of Fig. 1, showing the depression of the yolk cells to form the dorsal lip. S.C., segmentation cavity; BL., blastopore; M, cells which are to develop into mesoderm.

In opposition to most investigators, Moquin-Tandon (15), Houssay,

Robinson and Assheton (20), and Marshall (14) maintain that the archenteron of the amphibian embryo is not formed by a process of invagination, but by a splitting between yolk cells which thus form the dorsal as well as the ventral wall of the archenteron. In a later paper, Assheton (1)

states that "the formation of the primitive archenteron is by a process of splitting, and is the direct effect of the primary center of growth; whilst the continuation of the cavity produced by an overgrowth is the direct effect of the secondary center of growth."

That the archenteron in the egg of *Bufo lentiginosus* is not formed by a splitting between yolk cells is shown, I think, by a study of a series of well-preserved eggs during the early stages of gastrulation.

The archenteron never appears "slit-like" at this time.

On the contrary, its walls are usually some distance apart and its inner end is invariably rounded (Figs. 10, 11). Occasionally at the stage of Fig. 12, never earlier, I have seen an irregular cleft between the yolk cells at the anterior end of the archenteron which might, perhaps, be considered a forward extension of the

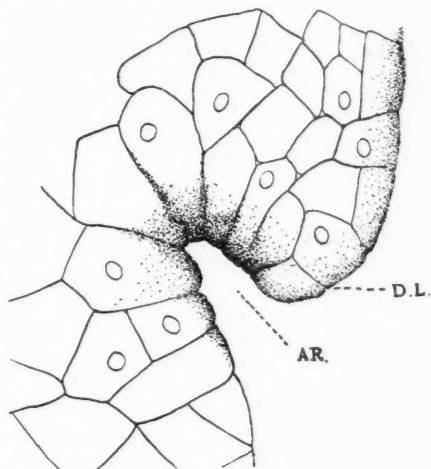


FIG. 10. — Part of a median section through the blastopore at a slightly later stage than Fig. 9, showing the character of the cells at the base of the blastopore furrow. *D.L.*, dorsal lip of the blastopore; *AR.*, beginning of the archenteron.

archenteron, but such a cleft is usually seen only in badly preserved eggs where the cells are all more or less separated, and therefore I have always considered that it was artificially produced by the method used in killing and hardening the egg.

Jordan, Wilson, and Eycleshymer (4), among others, have watched the disappearance of individual surface cells under the dorsal lip of the blastopore in the early gastrulation stages of the living egg. These observations seem to me to afford conclusive evidence that invagination of cells plays an important rôle in the formation of the archenteron.

The presence of pigment in the inner ends of the cells forming the dorsal wall of the archenteron has been explained by Robinson and Assheton as follows: "The pigmented area is produced and extended by the deposit of pigment in the adjacent margins of a double row of yolk cells which eventually will form the boundary wall of the archenteron, and it

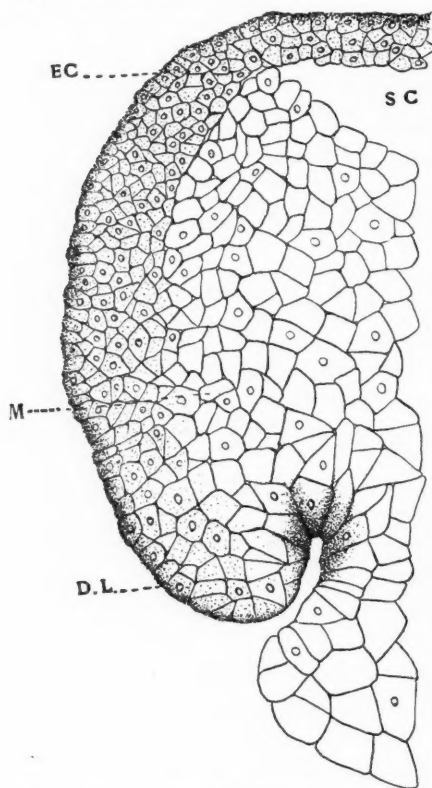


FIG. 11.—Part of a median sagittal section through the blastopore at the stage of Fig. 2. *EC*., ectoderm. Other lettering as in previous figures.

also radiates from this area along the adjacent margins of the cells of each row. A slit-like space appears in the middle of the posterior portion of the pigmented area. This space first limits the dorsal lip of the blastopore, and then extends forward and ventrally, following the deposit of pigment, and separating the two rows of marginally pigmented cells from each other." During the early stages of gastrulation there is always found at the anterior end of the archenteron a marked accumulation of pigment that is extended around to include a few of the yolk cells in this region (Figs.

10–12). I have never found more than a few scattered pigment granules in the lower yolk cells except in this particular part of the egg, and, if the archenteron is formed by a splitting

between marginally pigmented yolk cells, then the pigment must at once almost entirely disappear on one side of the split and not on the other.

The pigmentation at the anterior end of the archenteron in the egg of *Bufo* is not confined to "a double row of yolk cells" anterior to the actual cleft. Well-marked lines of pigment may extend out in any direction, even at right angles to the line of advance of the archenteron, as seen in Fig. 13. From the time that the blastopore is first formed, the pigment in the cells of the dorsal wall of the archenteron is always collected around the cell walls, never around the nucleus. Rhumbler (22) considers this phenom-

enon to be due to the mechanical effect of pressure. The suggestion has been offered by Jordan "that the pigment marks physiological activity, and that the less heavily pigmented cells of the ventral wall of the archenteron owe their relative lack of pigment to more sluggish metabolism attendant upon less rapid cell division." It is certainly true that the large yolk cells in the egg of *Bufo* divide less frequently than the cells in the upper hemisphere, but there is no evidence that the deeply pigmented cells of the outer surface of the upper hemisphere or of the dorsal wall of the archenteron divide more rapidly than the cells that are found between them. If, therefore, Jordan's suggestion is correct, some kind of

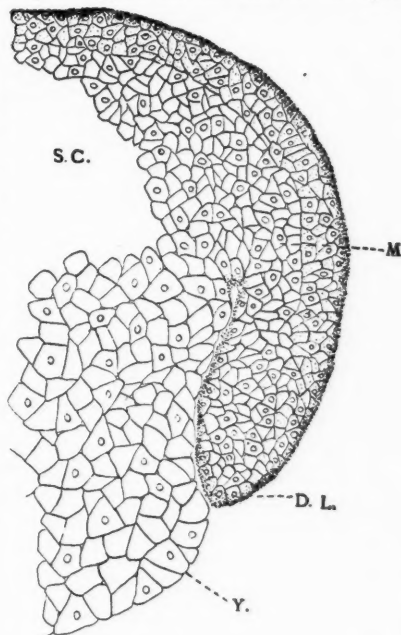


FIG. 12. — Part of a median sagittal section through the blastopore at the stage of Fig. 3. Y., yolk plug. Other lettering as in previous figures.

"physiological activity" other than that attendant upon rapid cell division must produce the pigmentation in these cells.

The extension of the lateral lips of the blastopore and the formation of the yolk plug have been so frequently described for other forms that a description of these processes is not necessary here, as they are apparently similar in all respects to those which take place in the frog. Following the method used by Pflüger (20), a number of eggs in the blastula stage were placed on a mirror in a shallow dish of water and the formation of the blastopore watched in mirror image. Figs. 1-8

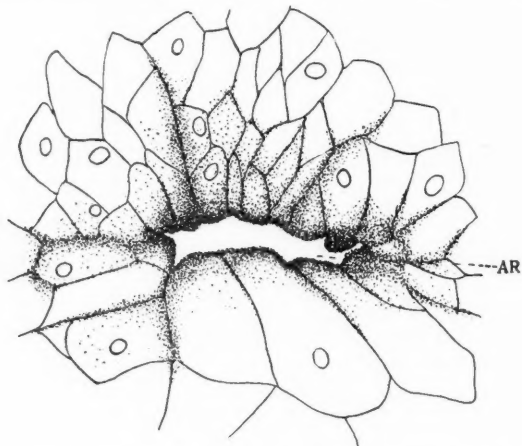


FIG. 13. — Part of a frontal section through the anterior end of the archenteron at the stage of Fig. 3, showing lines of pigment radiating out in all directions. *AR*, archenteron.

show the appearance and the location of the blastopore at different times during the day, from 8 A.M., when the blastopore lip first appeared, to 6 P.M., when the egg began a rotation around its horizontal axis. There was no evidence to show that the position of the eggs was changed during the time they were kept under observation; on the contrary, one egg, in which a peculiar light spot was seen below the equatorial region, was watched particularly, and the spot was found to keep its same relative position until the rotation of the egg took place. These mirror images show that the dorsal lip of

the blastopore appears below the equator of the egg at the edge of the black cells (Fig. 1), and that the blastopore rim extends at a uniform rate in the form of a crescent around the lower hemisphere, until finally the yolk plug is formed (Figs. 2-4). Meanwhile, the dorsal lip of the blastopore has moved over the yolk, and seven hours after its first appearance has reached the center of the white hemisphere (Fig. 6). The closure of the blastopore lips takes place almost uniformly from all sides as a rule (Fig. 7), although occasionally the blastopore is somewhat oval when it is in the stage of Fig. 8. At or just before the stage of Fig. 8 a rotation of the egg around its horizontal axis takes place, thus bringing the dorsal lip of the blastopore back to its original position.

In its movement over the lower hemisphere the dorsal lip of the blastopore seems to pass through about 140° of the surface of the egg. There is apparently a slight variation in this respect in different eggs. This measurement is somewhat greater than that given by Morgan (16) and by Wilson (27) for the movement of the dorsal lip of the blastopore in the frog egg, and differs considerably from the measurements which have been given by other investigators. Roux (21) and Pflüger (19) estimate that the dorsal lip moves about 170° , while Kopsch (11) considers the movement to be but 75° ; and this figure is further reduced by Assheton, who states that much of the so-called movement of the dorsal lip is only apparent and that the real movement is only from 60° to 70° .

THE FORMATION OF THE "GERM LAYERS" AND THE NOTOCHORD.

Observations regarding the origin of the endoderm, mesoderm, and notochord in different amphibian eggs are so conflicting that apparently the most plausible interpretation of them is to assume that there is absolutely no uniformity in the manner of formation of these structures even in species that are considered to be very nearly related to each other. Such an assumption, however, can scarcely be the correct one.

Goette (6), one of the early workers on the development of the amphibian egg, considered the mesoderm in the egg of *Bombinator* to arise from the splitting off of a layer of cells from the primitive entoblast, the layer thus formed extending as an unbroken sheet across the dorsal wall of the archenteron. The rest of the primitive entoblast was said to form the endoderm. According to Goette, a central chord of mesoderm in the mid-dorsal region of the embryo separates from the two lateral sheets to form the notochord.

A few years later Hertwig (7), after studying the development of the eggs of Triton and of *Rana temporaria*, came to the conclusion that the mesoderm in the amphibian egg arises in the vicinity of the blastopore "durch eine paarige Einfaltung des Entoblast schon zu einer Zeit wo die Gastrula-einstülpung noch nicht ganz vollendet ist." The amphibian egg was thus brought into agreement with Hertwig's observations on the development of other vertebrates and gave additional support to his well-known coelom theory. A few other writers — Balfour (2), Marshall (14), and Schwink (26) — agree with the results obtained by Hertwig.

In 1888, Schultze (25), from observations on *Rana fusca*, decided that "das mittlere Blatt, sowie die dorsale Urdarmwand entstehen aus dem Ektoblast und gehen an der dorsalen Urmundlippe alle drei Blätter in einander über; in den seitlichen und ventralen Theilen des Blastoporus setzt sich die Deckschicht des äusseren Keimblattes mit besonderer Klarheit in den Entoblast, die Grundschrift des Ektoblast ohne Unterbrechung in den Mesoblast fort." Perenyi (18), from observations on the egg of *Bombinator igneus*, Lwoff (13), from a study of Axolotl and various Anura, and Brauer (3), from investigations on two species of Gymnophiona, also came to the conclusion that the mesoderm is ectodermal in origin. These investigators, however, differ somewhat regarding the manner in which this process is supposed to take place.

Perenyi states that, as a result of a turning under, or "Duplikation," of the three-layered outer wall of the egg at the lips of the blastopore, "die äussersten Deckzellen der Blastula in ihrer ununterbrochenen Fortsetzung nach innen endlich die untersten

Zellenreihen bilden werden d. h. sie verwandeln sich in Entoderm, während die anderen zwei Zellenreihen der Blastula auch in ihrer Rückwindung beisammen bleiben und eine selbständige Schichte, das Mesoderm, bilden."

According to Lwoff, "die Einwanderung der Ektodermzellen und die Verschiebung der Entodermzellen zwei verschiedene und von einander unabhängige Vorgänge sind. Die Einwanderung von Ektodermzellen beginnt an der Stelle die das Hinterende des Embryo markirt; die Verschiebung der Entodermzellen beginnt im Gegentheil im vorderen Theile. Wie die weiteren Stadien lehren, bildet das Hineinwachsen der Ektodermzellen die zusammenhängende ektoblastogene Anlage der Chorda und des Mesoderms; die Verschiebung der Entodermzellen führt zur Bildung der Darmhöhle, die infolge des Auseinanderweichens der Entodermzellen entsteht."

Brauer's investigations show that there is a turning under of the outer surface cells, or "animal cells," at the posterior end of the germ disk and that by the forward growth of these cells under the upper animal cells a blind sac is formed. This blind sac becomes the posterior part of the archenteron, and at first its dorsal wall is composed of the animal cells invaginated from the surface. In subsequent development a layer of vegetative or yolk cells grows up from either side of the archenteron and forms a layer of endoderm beneath the invaginated animal cells which later become the mesoderm.

The origin of the mesoderm in the frog's egg has been described by Morgan (16) as follows: "The cells that are to form the mesodermal layer are present at the time when the dorsal lip of the blastopore has first appeared, and even just prior to that time." The innermost of the cells forming a ring around the equatorial region of the egg where the black and the white cells meet are the cells that later become the mesoderm. "These cells are carried up to the median dorsal line of the embryo by the closure of the blastopore. They will then be found forming a layer or sheet of cells that separates itself on the outer side from the thick layer of small ectodermal cells (that has been simultaneously lifted up) and that is

separated on the inner surface, but not very sharply if at all, from the dorsal and dorsal-lateral walls of the archenteron."

In the egg of *Bufo lentiginosus*, when the blastopore first appears as a slight depression among the yolk cells just below the equator of the egg (Fig. 9), the cells which form the dorsal wall of the segmentation cavity are all small, somewhat angular cells which contain a considerable amount of pigment, particularly the cells which compose the outer surface of the egg. Near the equator the cells are found to be somewhat larger and to contain much less pigment, while in the lower hemisphere the cells are very large, and they have but a few scattered pigment granules. Up to this stage of development there is no visible separation of the cells into ectoderm, endoderm, and mesoderm. The smaller cells resulting from rapid cell division are found in the upper part of the egg and the larger cells, which divide less frequently, are grouped around the lower pole. The mass of cells marked *M* in Fig. 9 undoubtedly represent the region of the egg from which the mesoderm is formed. These cells are in no wise distinctive at this period, and their later development into mesoderm I consider to be due solely to their position in the egg during the formation and closure of the blastopore. The cells which are to become mesoderm form a layer around the egg at the equatorial region just inside the cells that are to become the ectoderm, as found to be the case in the frog's egg, according to Morgan. These mesoderm cells have many characteristics in common with the large yolk cells into which they grade, being larger, more rounded, and containing much less pigment than the small cells of the upper hemisphere. It seems probable, therefore, that they were originally produced by divisions of the yolk cells.

When the lips of the blastopore have extended so as to form a crescent in surface view (Fig. 3) a frontal section through an egg in the region of the blastopore (Fig. 14) shows that the dorsal wall of the archenteron is formed of several layers of small cells which have absolutely no distinction between them except that the cells of the outer layer, which are more regularly arranged, contain a much greater amount of pigment than the other cells. At the sides of the archenteron the innermost

of these cells pass into the large yolk cells which form the floor of the archenteron. A median sagittal section through the blastopore at the same or a slightly earlier stage of development (Fig. 11) shows the beginning of the separation of the ectoderm from the inner cells of the egg. A tolerably regular cleft extends some distance around the sides of the egg, on a line usually with the lower edge of the dorsal wall of the segmentation cavity, sharply separating the layer of cells forming the outer wall of the egg from the cells within. The separation of the ectoderm does not extend as far down as the equator of the egg at this time, and it is some hours later before

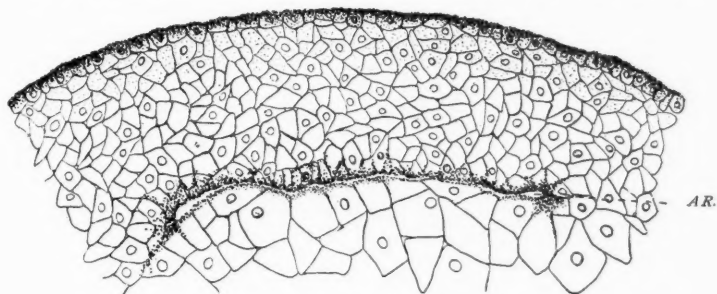


FIG. 14.—Part of a frontal section through the region just anterior to the blastopore at the stage of Fig. 3. *AR.*, archenteron.

the ectoderm at the lips of the blastopore is distinct from the other cells. It is in the region of the blastopore that the union of the different layers persists longest, as other investigators have noted.

At the stage of Fig. 3 the formation of the archenteron is well advanced, and a median sagittal section through the blastopore (Fig. 12) shows that the endoderm of the dorsal wall of the archenteron is formed of small, angular, deeply pigmented cells which, as far as I am able to determine, appear exactly like the small cells which form the outer surface of the egg. It seems probable that these cells once formed a part of the outer surface of the egg in the region just outside of the blastopore, and that they have been turned under the edge of the blastopore lip by a process of invagination, thus being changed into endoderm. Whether, in later stages of development, the endoderm

of the dorsal wall of the archenteron receives additions from the yolk, as believed to be the case by Assheton and by Wilson, I have not been able to determine.

After the ventral lip of the blastopore has formed and the blastopore is beginning to close (Fig. 6), a division of the

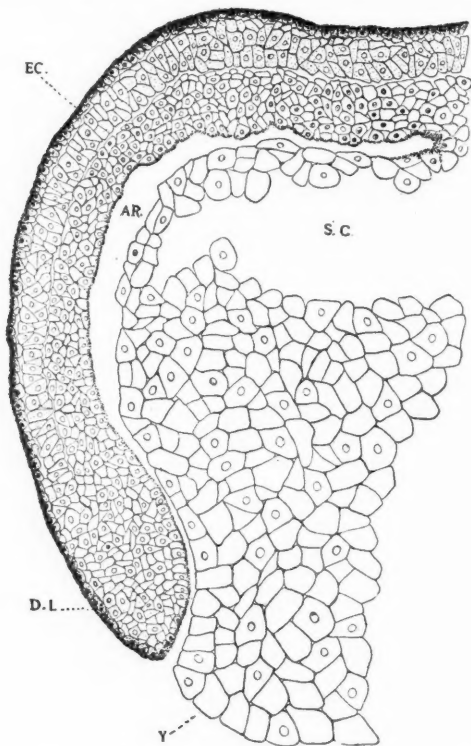


FIG. 15. — Part of a median sagittal section through the egg at the stage of Fig. 6.
Lettering as in previous figures.

ectoderm into two layers is first noticed. A median sagittal section at this period (Fig. 15) shows an outer ectodermal wall composed of a single layer of small, deeply pigmented cells which are arranged very regularly. The inner ectodermal sheath is composed of two or three layers of much larger cells

which are distinctly wedge-shaped and contain a comparatively small amount of pigment. The inner layer of ectoderm is sharply separated from the mass of small cells above the dorsal wall of the archenteron.

When, in surface view, the blastopore has reached the stage of Fig. 6, or in some cases even as early as Fig. 5, a splitting is seen in the mass of cells above the archenteron, and a single layer of endodermal cells is separated from the cells above.

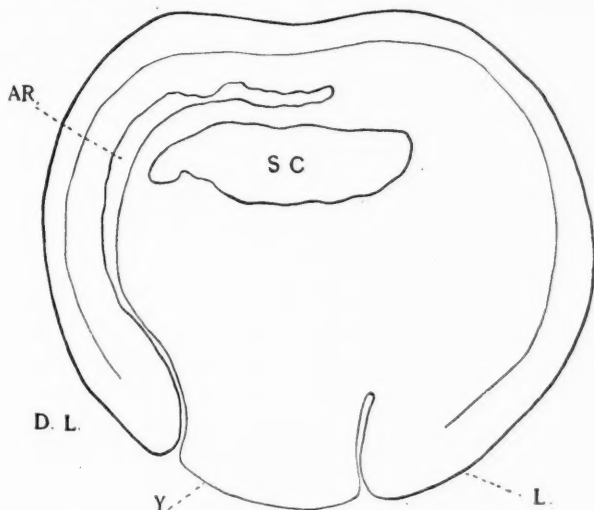


FIG. 16. — Outline of the entire section from which Fig. 15 was drawn.
L., ventral lip of the blastopore.

This process begins some distance in front of the region of the blastopore and gradually extends forward and backward from this point, thus completing the separation of the cells in the mid-dorsal region of the embryo into ectoderm, mesoderm, and endoderm.

When the blastopore has nearly closed (Fig. 8), a sagittal section through the middle of the dorsal lip (Fig. 17) shows that the endoderm cells of the dorsal wall of the archenteron (Fig. 17, *En.*) have flattened out considerably, and that they still contain much pigment, which is collected in the end of

the cell bordering the cavity of the archenteron. Above the endoderm is the mesoderm layer (Fig. 17, *M.*), which varies in the number of its cells in different parts of the egg. Near the dorsal lip of the blastopore the mesoderm sheath consists

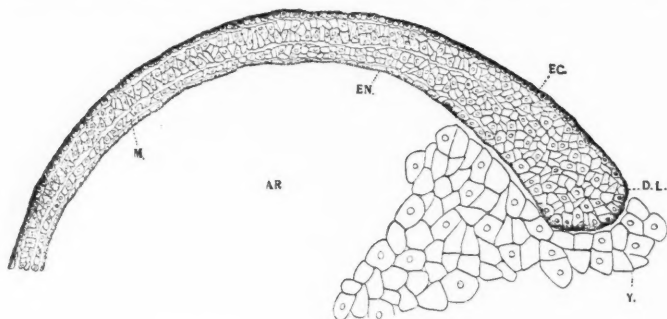


FIG. 17.—Part of a median sagittal section through the egg at the stage of Fig. 8. *EN.*, endoderm. Other lettering as in previous figures.

of several layers of small cells which are not pigmented. Forward from this region the mesoderm gradually thins out until it is composed of only a single layer of rounded cells lying between the endoderm and ectoderm; then it gradually becomes thicker again, and near the ventral lip of the blastopore it appears very much as it does near the dorsal lip, being composed of several layers of cells.

A frontal section through the middle of an egg at the stage of Fig. 7 shows a single layer of mesoderm over the dorsal region of the embryo, which gradually becomes several layers thick at the sides of the archenteron (Fig. 19), and below the archenteron passes directly into the yolk cells of the lower part of the egg. Still later stages during the closure of the blastopore show that the mesoderm is unquestionably extended at the expense of the yolk cells lying just beneath the ectoderm. Soon after the medullary folds have appeared the lateral sheets of mesoderm become fused on the ventral side of the embryo; thus a continuous sheet of mesoderm is formed around the embryo, except in the mid-dorsal region where the notochord has by this time been cut off from it. The extension of the

lateral sheets of mesoderm by a process of splitting off from the outer yolk cells has been noted by Schwink (26) in *Bufo vulgaris*, by Scott and Osborn (23) and by Jordan in the newt, and by Morgan in the frog.

At the close of the blastula stage a very large segmentation cavity is found in the upper hemisphere of the egg directly under the black pole (Figs. 9, 11, 12). During the formation of the archenteron this segmentation cavity decreases considerably in size, and is pushed out of its position, coming to lie below the archenteron and being separated from it by only a thin layer of cells (Fig. 16, S.C.). During the closure of

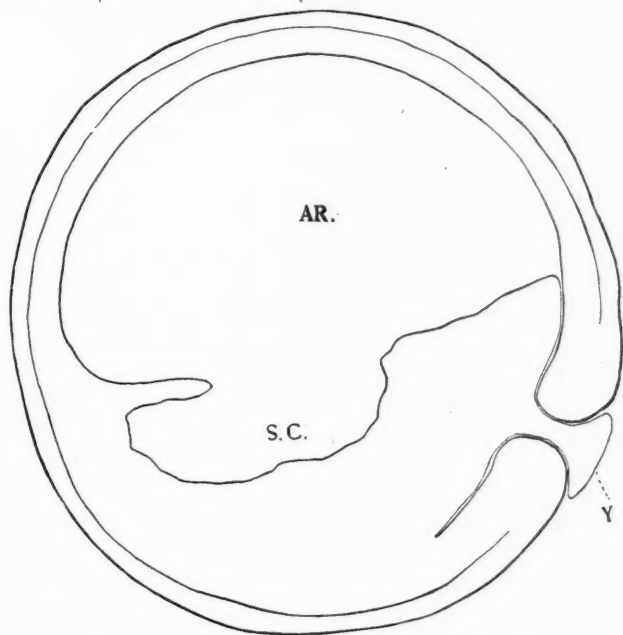


FIG. 18. — Outline of the entire section from which Fig. 17 was drawn.

the blastopore the archenteron increases greatly in size, and there is then usually but a single layer of large yolk cells between it and the segmentation cavity (Fig. 19). When the blastopore is nearly closed, I have frequently found eggs in

which there appeared to be a direct connection between the two cavities which could not be due to poor preservation of the material (Fig. 18). It would seem, therefore, that in some cases the archenteron is extended at the expense of the segmentation cavity, as supposed to be the case by Kupffer (12) and by Marshall.

A series of frontal sections through the embryo at about the stage of Fig. 7 will show the various steps in the forma-

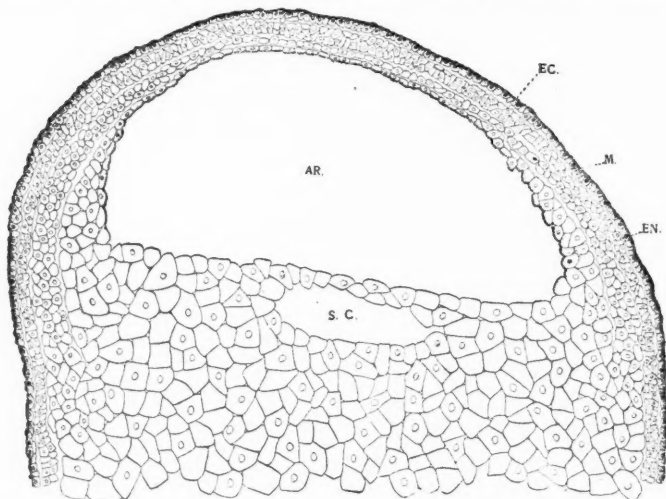


FIG. 19. — Part of a frontal section through the middle region of an egg at the stage of Fig. 7, showing the growth of the mesoderm at the expense of the yolk. Lettering as in previous figures.

tion of the notochord. A section just in front of the dorsal lip of the blastopore (Fig. 20) shows that the mesoderm in this region forms a continuous sheath over the dorsal wall of the archenteron and that it is composed of three to four layers of small cells (Fig. 20, *M.*). About eight sections anterior to Fig. 20 there is a noticeable thickening of the mesoderm in the mid-dorsal region (Fig. 21), while on either side of this thickening the mesoderm usually consists of but two layers of cells. More anterior, the thickened part of the mesoderm layer is completely separated from the lateral sheets

as a distinct rounded structure, the notochord (Fig. 22, *N*). For only a short distance at this stage of development is the notochord entirely cut off from the mesoderm; beyond there

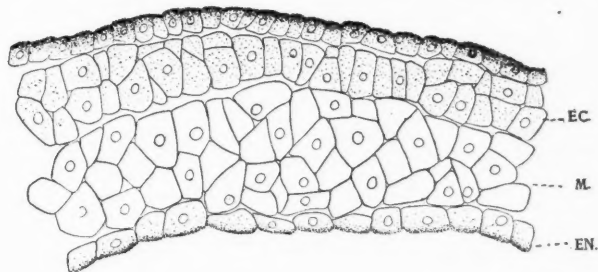


FIG. 20.—Part of a frontal section through an egg at the stage of Fig. 7, showing the mid-dorsal region of the embryo just in front of the blastopore. *EC*, ectoderm; *EN*, endoderm; *M*, mesoderm.

is the same thickening of the mid-dorsal portion of the mesoderm sheet as seen in Fig. 21. In the head region of the embryo the mesoderm is thinned out to a layer one or two cells deep which shows absolutely no thickening in the middle and appears very much as in Fig. 19. After the blastopore has closed, the notochord becomes extended forward in the head region and backward in the region of the tail.

Schultze, Goette, Lwoff, Brauer, Schwink, and Morgan also believe that the notochord is derived from the mesoderm; while

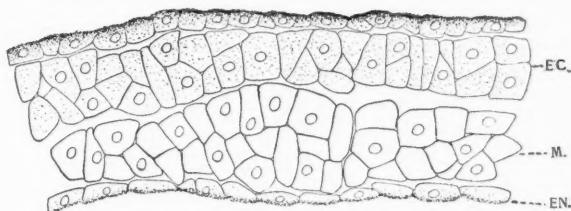


FIG. 21.—Part of a section from the same egg as Fig. 20 and slightly anterior to it. *EC*, ectoderm; *EN*, endoderm; *M*, mesoderm.

other investigators consider that in the amphibians, as in other vertebrates, the notochord is endodermal in origin. Although Field (5) believes that in *Bufo vulgaris* the notochord arises

from the endoderm, in the nearly related species, *Bufo lentiginosus*, the anterior part of the notochord is certainly mesodermal in origin. After the mesoderm layer has formed, the endoderm in the mid-dorsal region of the embryo is never more than a single layer of flattened cells. There is a closer connection between the mesoderm and the endoderm above the center of the archenteron than at the sides, but I have never found an egg in which these two layers could not readily be

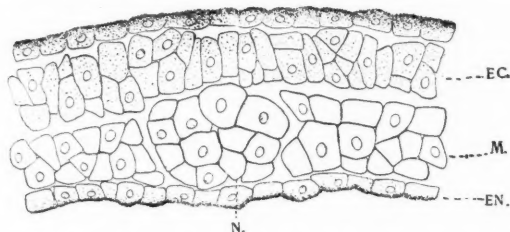


FIG. 22. — Part of a section from the middle region of the same egg. EC, ectoderm; EN, endoderm; M, mesoderm; N, notochord.

distinguished from each other. The endoderm cells are always much flattened at this period, and they invariably contain a considerable amount of pigment. The mesoderm cells and also the cells of the notochord are larger, more rounded, and contain but little pigment in comparison with the endoderm cells.

In conclusion, I wish to express my thanks to Prof. T. H. Morgan for advice and criticism during the progress of my work.

BRYN MAWR COLLEGE, BRYN MAWR, PA.,
December 16, 1901.

LITERATURE.

1. ASSHETON, R. On the Growth in Length of the Frog Embryo. *Quart. Journ. Micr. Sci.* Vol. xxxvii. 1894.
2. BALFOUR, F. M. Comparative Embryology. II. New York, The Macmillan Company, 1880.
3. BRAUER, A. Beiträge zur Kenntniss der Entwicklungsgeschichte und der Anatomie der Gymnophionen. *Zool. Jahrb.* Bd. x. 1897.
4. EYLESHYMER, A. C. The Early Development of Amblystoma, with Observations on Some Other Vertebrates. *Journ. Morph.* Vol. x. 1895.
5. FIELD, H. H. Bemerkungen über die Entwicklung der Wirbelsäule bei den Amphibien; nebst Schilderung eines abnormen Wirbelsegmentes. *Morph. Jahrb.* Bd. xxii. 1895.
6. GOETTE, A. Die Entwicklungsgeschichte der Unke. Leipzig, 1875.
7. HERTWIG, O. Die Entwicklung des mittleren Keimblattes der Wirbelthiere. I, II. Jena, 1881, 1883.
8. HOUSSAY, F. Études d'embryologie sur les vertébrés. *Arch. de Zool. Exp. et Génér.* Tome viii. 1890.
9. JORDAN, E. O. The Habits and Development of the Newt. *Journ. Morph.* Vol. viii. 1893.
10. KING, H. D. The Maturation and Fertilization of the Egg of Bufo lentiginosus. *Journ. Morph.* Vol. xvii. 1901.
11. KOPSCH, F. Beiträge zur Gastrulation beim Axolotl und Froschei. *Verh. Anat. Gesellschaft.* 1895.
12. KUPFFER, C. Die Entstehung der Allantois und die Gastrula der Wirbelthiere. *Zool. Anzeiger.* Bd. ii. 1879.
13. LWOFF, B. Die Bildung der primären Keimblätter und die Entstehung der Chorda und des Mesoderms bei den Wirbelthieren. *Bull. de la Soc. Imp. des Nat. de Moscou.* Bd. viii. 1894.
14. MARSHALL, A. M. Vertebrate Embryology. New York, Putnam, 1893.
15. MOQUIN-TANDON, G. Recherches sur les premières phases du développement des batraciens anoues. *Ann. des Soc. Nat.* Tome iii. 1876.
16. MORGAN, T. H. The Development of the Frog's Egg. New York, The Macmillan Company, 1897.
17. MORGAN, T. H., and TSUDE, UME. The Orientation of the Frog's Egg. *Quart. Journ. Micr. Sci.* Vol. xxxv. 1893.
18. PERENYI, J. Die Entwicklung der Keimblätter und der Chorda in neuer Beleuchtung. *Anat. Anzeiger.* Bd. iv. 1889.
19. PFLÜGER, E. Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen. *Pflügers Archiv.* Bd. xxxii. 1883.

20. ROBINSON, A., and ASSHETON, R. The Formation and Fate of the Primitive Streak with Observations on the Archenteron and Germinal Layers of *Rana temporaria*. *Quart. Journ. Micr. Sci.* Vol. xxxii. 1891.
21. ROUX, W. Ueber die Lagerung des Materiales des Medullarrohres im gefurchten Froschei. *Anat. Anzeiger.* Bd. iii. 1888.
22. RHUMBLER, L. Physikalische Analyse von Lebenserscheinungen der Zelle. III. Mechanik der Pigmentzusammenhäufungen in den Embryonalzellen der Amphibieneier. *Arch. f. Entwicklungsmechanik.* Bd. ix. 1899.
23. SCOTT, W. B., and OSBORN, H. F. On Some Points in the Early Development of the Common Newt. *Quart. Journ. Micr. Sci.* Vol. xix. 1879.
24. SCHULTZE, O. Zur Entwicklung des braunen Grasfrosches. *Festschrift f. Kölliker.* 1887.
25. SCHULTZE, O. Die Entwicklung der Keimblätter und der Chorda dorsalis von *Rana fusca*. *Zeitschr. f. wiss. Zool.* Bd. xxvii. 1888.
26. SCHWINK, F. Ueber die Entwicklung des mittleren Keimblattes und der Chorda dorsalis der Amphibien. München, 1889.
27. WILSON, H. V. Formation of the Blastopore in the Frog Egg. *Anat. Anzeiger.* Bd. xviii. 1900.

NOTES ON THE CŒLENTERATE FAUNA OF WOODS HOLE.

CHARLES W. HARGITT.

THE following notes upon certain faunal features of the cœlenterate life of Woods Hole and adjacent waters pertain chiefly to the season just past, including records which are fairly constant at regular intervals throughout the entire year. For certain of them I am indebted to Mr. Vinal Edwards, whose painstaking records during many years are matters well known to many naturalists. I am also under obligations to Mr. George M. Gray and Dr. H. M. Smith for similar favors. In addition to notes upon the seasons, habits, etc., brief accounts are presented of new forms discovered and of the development of one of the Scyphomedusæ.

HYDROMEDUSÆ.

A New Tubularian Hydroid.—In August, 1900, while cruising and dredging in Muskegat Channel off Marthas Vineyard, a considerable number of fine specimens of *Corymorpha pendula* Ag. were taken by dredge and trawl, many of which were in fine condition, still imbedded in the sand as in normal life. A somewhat cursory examination of the specimens showed what seemed to be young specimens growing among the filamentous rootlike holdfasts and apparently budding from the base of the hydroid, like young polyps, reference to which fact was made by the present writer in the recently published synopsis of Hydromedusæ. In order to determine more definitely the apparent anomaly of buds arising from so low among the rhizoids and below the sandy surface of the substratum, and whether they might show signs of later becoming detached, the specimens were submitted to one of my students, Mr. A. J. May, with instructions to determine the range of budding, nature of

development, etc. The results have shown what was only at first dimly suspected, namely, that the small "buds" were in fact not buds at all, but a distinct hydroid, apparently parasitic, growing upon the base of the *Corymorpha*. This was clearly demonstrated both from the specific differences which a critical study of its morphology showed, and by means of sections made through the points of attachment. The point of attachment is within a rather limited zone of the base, among the conical papillæ and filamentous rhizoids of the host, where in some cases as many as half a dozen were growing upon the same

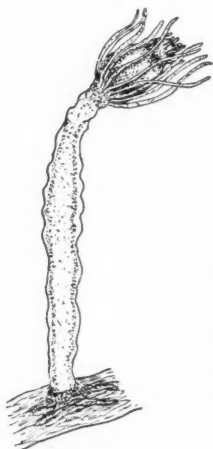


FIG. 1. — *Tubularia parasitica*.

specimen. As will be noted from Figs. 1 and 2, the new hydroid clearly belongs to the genus *Tubularia*, having the characteristic form of body, arrangement of tentacles, etc. Its attachment to the host was quite close, being inserted within the filmy perisarc, where its base expanded in the form of fingerlike absorbent organs.

Briefly its characters may be summarized as follows: Hydranth solitary, from 2 to 5 mm. in height and about $\frac{1}{8}$ mm. in diameter; tentacles in two whorls, the proximal of from eight to sixteen, the distal of from five to eight. Gonads were found upon but one specimen, and in this were immature, but occupying the characteristic position among the basal tentacles. So far as known, semi-parasitic upon *Corymorpha*. I propose for it the provisional name *Tubularia parasitica*, till further investigations may be had upon additional and more mature specimens, which may further confirm or modify this description.

A New Hydromedusa. — On Aug. 10, 1901, a medusa with distinctively sarsian characters was taken in the tow, similar in many respects to two species described by Forbes in 1848 (British Naked-Eyed Medusæ), chief among their features being the proliferous development of medusæ from the body or manubrium of the parent medusa. Haeckel likewise described a similar medusa

from the Canary Islands, in which secondary medusæ were budded in great numbers from the very long siphonlike manubrium. So far as I am aware, no member of the genus *Sarsia* having similar characters has been described from American waters.

Forbes's species were *Sarsia gemmifera* and *S. prolifera*, as cited above, pp. 57-59. The former, like Haeckel's *S. siphonophora*, buds its secondary medusæ from the walls of the long manubrium in a spiral-like raceme throughout its entire length. In the specimen under consideration the proliferous medusæ are budded from the manubrium, but in a whorl about its base (cf. Fig. 3). Only a single specimen was taken, but its characters were so definite that there seems little doubt as to its specific distinctness.

The following characters summarize its more distinctive features: Bell high, somewhat ovate, or elongate hemispherical; tentacles four, with prominent basal bulbs, orange-colored, with marginal fringe of delicate green, each bulb with a prominent ocellus densely black and facing outward. Manubrium long, pendulous, extending far beyond the margin of bell, capable of great contraction; terminal portion doubly

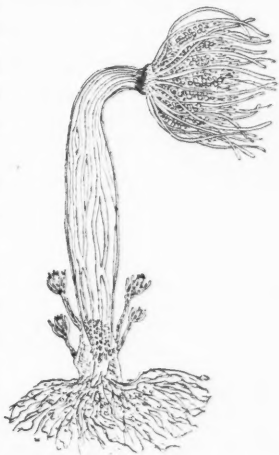


FIG. 2. — *Corymorpha pendula* Ag. with *Tubularia parasitica*.

bulbous, with proximal bulb light sky-blue, terminal green; basal portion of manubrium expanding into an orange-colored gastric pouch which graduates into the body of the bell. Gonads medusoid, in a whorl about the base of the manubrium; ectoderm transparent or faintly tinged with pale blue, entoderm orange-colored. Height of bell, 1.5 mm.; breadth, 1 mm.

For this medusa the name *Coryne producta* is proposed. The description is based upon a single specimen, and while its characters seem sufficiently definite to warrant specific distinction, it is not impossible that other specimens in larger numbers may necessitate modification or change at certain points.

SEASONAL ASPECTS.

The seasonal range among medusæ is noteworthy in many cases, both by reason of its periodicity in certain species and by its perennial character in others. The following are among the distinctively spring medusæ.

Hybocodon prolifer Ag. is one of the most restricted in this respect, ranging from late February to about the middle of May. It is one of the most beautiful and brilliant of the early medusæ. Its proliferous budding of secondary medusæ from the large single tentacle is an interesting and well-known feature. I have also found it producing actinulæ from the

walls of the manubrium at the same time. These seem to arise much as do similar larvæ, from several other anthomedusa, and a histological examination shows essentially similar features of oögenesis and spermatogenesis, though there is no appreciable distinction of sexes so far as morphological features are concerned.

Tiaropsis diademata Ag. This is likewise an early medusa. According to Agassiz, "one of the earliest visitors of our wharves in spring." During the present season it has been taken from March 20 to May 1, though only in limited numbers.

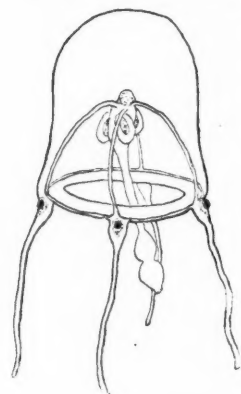


FIG. 3. — *Coryne producta*.

Coryne mirabilis Ag. is also one of the earlier medusæ, but with a longer range, from February to May. It has been reported by Fewkes as occasionally taken at Newport in early summer.

Lizzia grata A. Ag. Of this medusa I have records during the present year from March 27 to April 29. Fewkes has reported it as occurring at Newport during the entire summer, but this would seem to be somewhat unusual.

Tima formosa Ag. This beautiful medusa, one of the largest of the early Hydromedusæ, while not specially rare at

this station, is not specially abundant. Its season is comparatively brief, ranging from April 12 to May 5. While sometimes quite abundant at certain localities, its hydroid phase is as yet unknown, as is also its development.

Trachynema digitale A. Ag. This Trachomedusa is occasionally taken here in considerable numbers in April, but is not a common medusa. Little appears to be known as to its habitat or life history, but it is probably more or less pelagic, and hence subject largely to the influence of ocean currents, etc.

Rhegmatodes tenuis A. Ag. Note is made in this connection of the occurrence of this medusa in large numbers during the summer of 1900, the first record during several years, and its utter absence during the present season. It is usually recognized as a summer medusa, and the present record only confirms this. What is more specially worthy of note is the erratic aspect of its appearance, apparently at long intervals, and then usually in great numbers, indicating seemingly some local or environmental condition as governing its occurrence, rather than purely seasonal mutations. Were Rhegmatodes a pelagic medusa we might account for mutations of this sort through the agency of shoreward currents or winds, as often happens with Physalia, and perhaps also with Trachynema, as intimated above. But so far as I am aware, this medusa, in common with most of the Hydromedusæ, is more or less restricted to the littoral fauna, and hence only incidentally affected by such influences. This is another medusa whose hydroid yet remains unknown. Possibly when its life cycle is fully known the apparent capriciousness of its occurrence may be cleared up.

Staurophora laciniata A. Ag. was likewise taken in considerable numbers in early May by Mr. George M. Gray, and later in the month by Dr. H. M. Smith. So far as my records are concerned, this is the first occurrence of this medusa in several years at this station. One of its peculiar structural features, the early confluence of the oral lobes with the frills of the gonads, so that they can only be distinguished with difficulty, was described by A. Agassiz. No mention, so far as I am aware, has been made of the origin of actinulæ in this

medusa by a method very similar to that of *Hybocodon*. In *Staurophora*, however, they arise within the greatly folded borders of the gonad pouches beneath the radial canals. As in the former, no conspicuous differentiation of sex was apparent in *Staurophora*, though not having seen them alive, and not having as yet examined the histology of the gonad region, this can only be stated tentatively.

Among medusæ taken during midsummer, the more common were *Nemopsis bachei* Ag., very abundant during August; *Bougainvillia carolinensis* Ag., likewise abundant during August; *Pennaria tiarella* McCr., less abundant than during previous seasons; *Ectopleura ochracea* A. Ag., unusually abundant during August, taken mostly in the evening tow; *Eucheilota duodecimalis* A. Ag., *Eucheilota ventricularis* McCr., not uncommon during August; *Eutima limpida* A. Ag., fairly common, but sexually immature; *Lafea calcarata* A. Ag., not uncommon, and in many cases the several phases in the development of the medusa were taken. *Dipurena conica* A. Ag. and *D. strangulata* McCr. were taken, but from a comparison the specimens so intergraded as to suggest a probability of their specific identity, with only varietal differences.

Of rarer medusæ the following were taken: *Willia ornata* McCr., taken in considerable numbers at various times during the summer, were evidently breeding, as medusæ of all sizes and stages of development were found; *Podocoryne carnea* Sars, taken sparingly; *Epenthesis folcata* McCr., not numerous, colors less brilliant than those figured by Mayer for this species. Species of *Obelia* were notably few during the present summer, in rather sharp contrast with previous records. It is one of the few medusæ with a record extending throughout the entire year and often occurring in immense numbers, this latter being common with many species of *Obelia*.

SCYPHOMEDUSÆ.

These medusæ were more than usually abundant during the summer, a thing not common at Woods Hole except very early. Many specimens of *Aurelia*, *Cyanea*, and *Dactylometra*

were taken about the docks of the fish commission during July, and even August, which were sexually mature, and from some of which ova were obtained and the development followed as described below. That these were not an isolated few left over from the earlier numbers of April and May is evident in that many were taken in the open waters of Vineyard Sound, and even in the open sea far from land in the region of the Gulf Stream, mostly of the genus *Cyanea*. They may have been caught up by southward currents from a more northern locality along the coast of Maine or beyond, and carried to these southern ranges.

Specimens taken into the laboratory and placed in aquaria discharged developing ova in great numbers, literally covering and packing the bottom of the aquaria. The following synopsis of the development of *Cyanea* may not be without interest as having been carried on under the wholly artificial conditions of the aquarium, from the later cleavage of the egg on to the freeing of the ephyrae, — a circumstance not hitherto recorded, so far as I am aware, though Bumpus has recorded the fact that earlier phases occur readily under such conditions, and both McMurrich and Hyde likewise refer to the same fact, but they do not seem to have succeeded in tracing the entire development.

The early cleavage phases of *Cyanea* are passed while the ova are still within the gastric cavity or while "nursed" within the ample folds of the manubrium or frilled oral margins. A typical blastula results from total and regular cleavage and appears to be followed by an early gastrulation and the prompt obliteration of the blastopore.

Soon after this, and while the larvæ are still within the egg membrane, cilia are developed, and they may be seen slowly rotating within the membrane, which, however, is early ruptured and the embryo escapes as a free-swimming organism. In shape it is at first almost spherical, but soon takes on the oval or pyriform shape characteristic of most planulæ. Details as to the origin and differentiation of the endoderm are not yet worked out, but they seem to conform rather closely with the observations of Hyde and the later conclusions of Smith

on Aurelia, as well as with the recent work of Hein on the same form.

The larval history seems to vary greatly as to matters of growth, transformation, etc. A few specimens attached themselves to the bottom of the aquaria in from six to ten days and promptly assumed the typical scyphistoma stage, while others were swimming planulæ at the end of as many weeks, showing no tendency toward transformation.

Encystment. — Both McMurrich and Hyde have recorded an encysting phase in the life of the planula preceding metamorphism. Hyde noted, however, that in one series of experiments this did not take place. My own observations have probably sufficed to reconcile these discrepancies by showing that it is incidental rather than essential, — a mere adaptation to changed conditions.

That encystment may and does occur under certain circumstances is not in the least doubtful, if not indeed a more or less common phenomenon in development under artificial conditions. A very considerable proportion of my own specimens passed through such a stage, which varies from a few days to many, and is, indeed, often a permanent and fatal one; but, on the other hand, it is not less certain that many passed through the metamorphoses without the least sign of encystment, while in others there was the aspect of incipient encystment common in many hydroid planulæ, namely, the secretion of a delicate perisarc-like sheath over the base of the planula in the process of attachment. There seems little doubt, therefore, that in these variable aspects we have the clue to the entire matter, so far as these larvæ are concerned, and may consider encystment, as above intimated, to be an adaptation against unfavorable conditions, and therefore comparable with the same phenomenon among Protozoa and other organisms. May it not hint the probable phyletic origin of the perisarc structure so largely characteristic of one class of cœlenterates, to which the facts under consideration may show more or less definite reversion?

The Scyphistoma. — The young scyphistoma is at first of vasiform shape, the base small and adherent by the delicate

film of horny secretion referred to above. The primary tentacles are usually four in number and arise as small buds from the broad oral end of the polyp about the same time as the mouth is formed. In many cases the number varies, only two arising at opposite sides, two others following at intermediate positions. More rarely only three tentacles occur in the primary set, followed by three others likewise in intermediate positions, giving the polyp at first a trimerous and later a hexamerous aspect, — a condition usually associated with the phenomenon of a triangular mouth which continued even during the entire history of the polyp. In several cases bifurcated tentacles occurred, and continued during the scyphistoma stage. The average number of tentacles is sixteen, though this may also vary considerably, many specimens being noted with twenty or more. The scyphistomæ of *Cyanea* are almost clear white in color, in rather marked contrast with the dull flesh color of the polyp of *Aurelia*, and when viewed in colonies against a black background present a most beautiful picture.

Stolonization. — This is a much less common feature in *Cyanea* than in *Aurelia*, though not by any means rare. Stoloniferous processes may arise from the bases or sides of the polyps, and growing laterally may become attached and serve as points of origin for new buds. They are, however, fewer in number and give rise to no such complex colonies as are frequent in polyps of *Aurelia*. No cases of the direct origin of secondary polyps from the body of the parent were noted in the case of *Cyanea*.

Strobilization. — Owing to the small size of the polyp of *Cyanea*, strobilization is comparatively inconspicuous and was only at first noted about the time the fully formed ephyra rendered the fact evident and directed attention to it. The segments are few in number, in many cases a single one only occurring at a time, though three or four are not unusual; but in no case were more than five noted upon any given specimen. In the cases of polystrobilous specimens the basal portion seemed to renew its activities, new tentacles arising and the specimen showing every indication of healthy development,

probably later strobilating as before, though no demonstration of this was undertaken.

The time involved between the attachment of the planula and the assumption of the strobila stage and the discharge of ephyrae was like that of the planula history, quite variable. The minimum time noted between the attachment of the planula and the assumption of the strobila stage was ten days, making the time from the origin of the planula to that of the strobila about seventeen days, or about eighteen to twenty days for the appearance of the ephyra. But as before intimated, there is much variation on this point, probably more than occurs in natural conditions.

The Ephyra.—Ephyrae liberated in the aquarium seemed quite normal in morphological aspects. In color they are dull brownish, the color showing itself as the strobilization proceeds toward maturity. In habit the young ephyra appears somewhat sluggish, and, while capable of active movement by the contractions of its bell, lies rather quiescent in the aquarium, seldom moving except as stimulated by agitation of the water or otherwise. While in rest it lies upon the aboral surface, with the manubrium extended upward, probably a condition assumed for the capture of prey.

Several specimens were marked by definite variation in the number of lobes or other organs. A specimen with nine lobes had also a similar number of rhopalia, while another with eight normal lobes had three extra rhopalia irregularly disposed at intermediate positions. Several specimens taken in the tow showed also similar variations, as did likewise several adult specimens taken during the summer and at previous times.

Feeding.—In rearing the polyps several experiments were made upon the feeding habits. Scrapings of slime, algæ, etc., from the eelgrass, which contained numerous Protozoa, were found to be among the most successful sorts of diet. Larvæ of gastropods and starfish were also taken readily by the polyps, the former especially being apparently quite acceptable. Diatoms and other micro-organisms taken from the deep waters of the Sound apparently proved deleterious, the polyps in aquaria supplied with this food showing evident and

rapid decline of vigor and health. In small aquaria numerous cases of cannibalism were noted, the scyphistomæ greedily devouring any planula which came within the grasp of the vigilant tentacles, the entire process of engulfing the victims being several times observed.

A Cubomedusa from Woods Hole. — Several specimens of an interesting medusa of this order were taken in the tow, the first on August 13, in Great Harbor, a second the following day at North Falmouth, Buzzards Bay. Two or three others were taken within the next day in Great Harbor.

In general features the medusa resembles very closely one figured by Mayer from the Tortugas (*Bull. Mus. Comp. Zool.*, Vol. XXXVII, No. 2, p. 70), and to a less degree a medusa described by Fewkes from the Bermudas (*Bull. Mus. Comp. Zool.*, Vol. XI, No. 3). In many respects, however, it differs from both, namely, in its larger size, deeper color, apparent absence of gastric filaments, figured by Mayer. Both Fewkes and Mayer consider the specimens taken by them as immature, and their identification was accordingly somewhat doubtful, the former assigning his to the genus *Tamoya*, the latter referring his, together with that of Fewkes, to the genus *Charibdea*. Certain it seems that unless the specimens are immature they could hardly be included within either genus, or indeed within any other of the at present recognized genera of the family. The absence of velar canals and pedalia, as well as the very short tentacles, would of themselves be sufficient to exclude them.

The same is likewise true of the specimens under consideration. They are so nearly identical in morphological features, size, etc., as to suggest something like maturity, unless, perchance, they should be indigenous species, — an exceedingly doubtful supposition. If borne hither from the Tortugas or Bermuda by currents, it would seem that the time involved in transit should have given at least some differentials of size or other peculiarity.

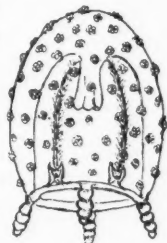


FIG. 4. — *Charibdea verrucosa*.

The following descriptive characters may serve to show in how far they fail to conform to the type characters of the genus: bell ovoid in profile, cuboid as seen from either pole; size from 2 to 3 mm. in short diameter by 4 to 5 mm. in height. Color a dull amber, somewhat translucent; exumbrellar surface dotted irregularly with light brownish warty clusters of nematocysts. Tentacles brown in color, rather short and spindle-shaped, with deep annulations. Rhopalia four, radially located, set in rather deep pockets somewhat above the level of the margin, each with several ocelli near the tip. Velarium well developed, and strengthened by four frenulae or thickenings of the subumbrella in the region of the radii. Absence of any traces of velar canals is noteworthy, as is likewise absence of mesenterial filaments. Distinct gonads could not be distinguished, though sections showed a genital region and ova in process of development. Manubrium well developed, quadrate in form. In case the specimens may be referred to the genus *Charibdea*, it must be upon the assumption of immaturity, as Mayer has suggested, in which case they compare fairly well with Mayer's *C. aurifera*, though in size somewhat larger and more brownish in color. If, as seems not unlikely, they must be given specific distinctness, I would propose for the species the name *verrucosa*, as significant of the warty knots of nematocysts which adorn the outer bell.

THE ZOOLOGICAL LABORATORY,
SYRACUSE UNIVERSITY, May 1, 1902.

THE BODY SENSE HAIRS OF LEPIDOPTEROUS LARVÆ.¹

WILLIAM A. HILTON.

It is well known that, as a rule, all arthropods have their bodies and appendages clothed with hairs, or setæ, which are simply modified parts of the cuticle.

These hairs vary in form and in structure. In the most common type the hair is hollow, and its lumen communicates with the body cavity by means of a "pore canal" in the cuticle (Fig. 1). Through this pore various structures may extend into the lumen of the hair, as a prolongation of a hypodermal cell, gland ducts, and nerves.

There are published references to solid hairs of insects; but if we except certain minute elevations of the cuticle, such as are represented in Fig. 2, and which are more or less hairlike, I found none in the insects studied. It should be said, however, that certain scalelike appendages of the cuticle of the larva of *Corydalis* (Fig. 3, *h*) appear to be solid; but as these occur, each at the end of a pore canal, they may prove to be hollow.

The most commonly observed structure that passes through the pore canal into a hollow hair is a prolongation of a hypodermal cell, which is much larger than the ordinary cells of the hypodermis (Fig. 4, *f*). Such a cell was named a "trichogen," by Graber, as it is believed to be the element that produces the hair. In many cases there are associated with the trichogen one or more gland cells, which discharge their secretion through the hair; the stinging hairs of certain larvæ are examples of this type. Such hairs may also have a nerve extending to them, and perhaps they always do.

A type of hollow hair which occurs much more commonly than does the glandular hair is one into the lumen of which

¹ *Contribution from the Entomological Laboratory of Cornell University.*

there extends only a trichogen cell and a nerve. The larger number of the organs of special sense of arthropods are hairs of this type, more or less modified. Frequently, however, the modification has been carried so far that the organ of special sense is not at all hairlike. This is especially true of many of the supposed organs of taste and of smell. I have made no attempt to study these.

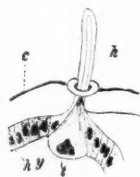


FIG. 1.—Simple hair from the silkworm (*Bombyx mori*).

The investigation, the results of which are given in this paper, was confined to a study of those hollow hairs, or setæ, which are distributed over the surface of the body and are believed to be organs of touch. The primary object of this investigation was to determine as definitely as possible just what type of hair on the body surface is a sense hair; a secondary object was to determine in what ways this type is modified in various lepidopterous larvæ. Some work was also done on several other orders of insects, with the result that a close correspondence was found in the structure of these hairs among even widely separated orders.

METHODS.

In order to definitely demonstrate which hairs were sensory it was necessary to have recourse to special histological methods, as the terminations of the nerves for touch in insects are exceedingly delicate, and the usual microscopical methods are entirely inadequate for the successful differentiation of the nervous tissues. For general anatomy of the sense hairs the usual fixing and staining fluids were used; but for staining the peripheral nerve fibers and cells the *intra vitam* methylen blue method

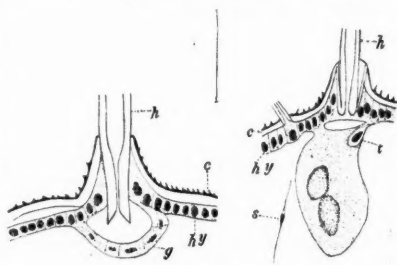


FIG. 2.—Sections through hairs from a tiger moth (*Spilosoma virginica*).

was found to be especially useful; and, as the larger part of the work was based upon results thus obtained, it may be well to give the exact method of procedure.

The fluid used for injecting was Grüber's B.x methylen blue, $\frac{1}{2}$ per cent solution in normal salt. The injection by means

of a small syringe was made usually in the side, back of one of the last abdominal segments, and enough liquid was injected to color the segments near the head, care being taken to insert the canula only under the hypodermis and muscles, and not into the alimentary canal.

After injection the animal was left quiet for a period of about

three hours for most insects, but with some, as with *Pieris*, two hours was a better time, and four hours seemed to be best for *Datana* larvæ. It is important that the insect remain alive during this period after injection.

When the proper period has elapsed the nerves and nerve cells should be well stained and almost all other tissues free from stain. After successful staining the specimen is cut open lengthwise and pinned out over a hole cut in sheet cork, the muscles and viscera are removed by careful dissection, and then, on examining under a microscope, the nerves and nerve cells are seen stained upon the surface of the unstained hypodermal layer. The bases of the hairs may be seen through the hypodermis, and it is easy to trace nerve cells and fibers in connection with them. By keeping the preparation wet with normal salt solution and using different powers of the microscope, much may be learned regarding the structure and distribution of the peripheral nervous system without further preparation; for this work the silkworm (*Bombyx*



FIG. 3.—Section of cuticle of *Corydalus cornuta*, showing large and small flat scales supplied with nerves and cells. All beyond edge of cuticle from Golgi preparation, the sensory cells and nerves demonstrated by methylen blue.

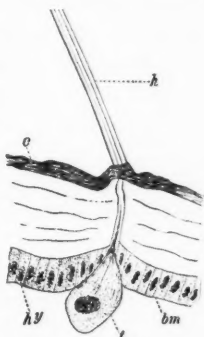


FIG. 4.—Section of hair of *Datana*.

mori) was very good, because the blue nerves on a pure white background stand out very clearly. Of course, such preparations last but a short time, fading out in an hour or less, and the ultimate distribution of the terminal nerve fibers cannot be seen without sectioning.

The following modification of Bethe's formula for fixation was used :

Ammonium molybdate	1 g.
Con. HCl	10 drops.
Dist. H ₂ O	100 cc.

This solution was used ice cold and allowed to act on the tissues from eight to twenty-four hours, after which they were washed well in cold distilled water and placed in absolute alcohol for about three hours, then cleared in xylene, and either mounted whole or imbedded and sectioned.

HISTORICAL.

Setiferous sense organs in arthropods were described by many early workers; but the first description of a bipolar nerve cell one termination of which was at the base of the hair and the other continued with the nerve trunk to the central nervous system was made by Leydig in 1851, for certain hairs of *Corethra plumicomis*. This discovery of Leydig was verified, and the form described is now generally regarded as the type of sensitive termination in arthropods. Leydig undoubtedly mistook the trichogen cells for nerve cells; these two elements were later distinguished by Hauser ('80) and Villanes ('81). Later works, especially of Retzius ('90-'95) and Vom Rath ('91-'96), brought forth the following results:

In arthropods all sensory terminations, the eyes excepted, are in hairs. To each hair there corresponds at a greater or less distance from the base one or more bipolar sense cells, of which the distal prolongation penetrates into the interior of the hair terminating without ramifying, the other prolongation (proximal) in a nervous center. These observations, which accord so well with other classic works on the peripheral nervous system, were made somewhat doubtful by more recent works.

In Crustacea, Bethe ('95) and Nusbaum ('97) recognized the sensory neuron as a bipolar cell, the distal portion penetrating the hair without ramifying and the other prolongation continuing with the nerve trunk; but, at the same time, they also described a plexus of cells, — not a system of neurons, but a true plexus. Bohumil Nemec ('96) found in certain isopods a system of peripheral ganglia. These ganglia are centers of a hypodermal plexus compared by him to the plexus of Bethe. Rina Monti ('93) described a similar plexus in insects, and Holmgren ('96) described and figured such a network of multipolar cells with their processes in the larva of a sphinx moth.

In '97 and '98 Duboscq summarized very well the results of many authors and added some of his own observations on Orthoptera and chilopods. He used both the Golgi method and methylen blue and discredits much of the former work on the nerve plexus obtained by methylen blue, and that on the termination of the nerves by the Golgi method.

SENSORY CELLS AND NERVES OF BODY SENSE HAIRS.

Following the sensory nerve trunks peripherally, they are seen to run straight out from the central nervous system, dividing dichotomously, most of the branches coming off when the region of the back is reached. After a number of divisions, small nerves from bipolar nerve cells join the larger trunks, and the peripheral parts of the larger nerves may also be traced to bipolar nerve cells (Fig. 5).

In the silkworm (*Bombyx mori*) bipolar nerve cells are spindle-shaped and have a very dark nucleus, which in many cases nearly fills the cell body (Figs. 5-6). In most forms studied the cells are more nearly spherical, but yet not markedly so (Figs. 5-6). As a general rule the sensory cell is quite a distance from its hair, but again in the myron sphinx there is a slight variation, the nerve cell being at the edge of the pore canal, almost in its cavity; this may not indicate that the nerve is really shorter, but only apparently so, because of the thickness of the cuticle and consequent length of the pore canal.

The prolongation of the nerve just beyond the sense cell is of considerable thickness, staining deeply; and abruptly after this the nerve extending to the hair is very minute.

It was impossible to trace the nerves farther than the bases of the hairs where whole mounts were made, and Duboscq ('97 and '98), in Orthoptera and chilopods, traced the nerves only this far. However, earlier workers with methylen blue who studied simply the surface views represent nerves coming from the tips of the hairs; but it seems probable that such figures are in large part diagrammatic. Vom Rath found by the Golgi

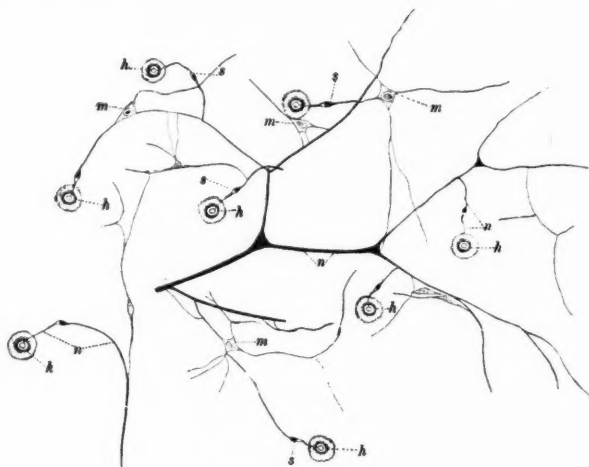


FIG. 5. — Surface view of subhypodermal nerves and cells from the silkworm (*Bombyx mori*). Bases of hairs also shown. Methylen blue.

method cavities of sensory hairs filled with nerves; this result is regarded as an artifact by Duboscq, who shows clearly how appearances like nerves may be obtained in the cavity of hairs due to deposits of chromate of silver; and he shows quite clearly that when nothing but the nerve cell and fiber is impregnated the nerve fiber stops at the base of the hair, as was apparently the case in his methylen blue preparations.

Retzius ('95), in *Astacus*, by means of the methylen blue method, traced the nerve to the base of the hair. This attracted the

attention of Bethe ('96), who investigated this point and found two sorts of hairs in *Astacus*, one as described by Retzius, in which the cavity of the hair was shut off at its base by chitin, and the other having its cavity freely open at the base. In the closed hair a nerve fiber was seen to stop at the base of the hair, but in the open hair it was continued a short distance into the shaft, and he suggests that probably this fiber goes nearer the tip than was observed in the specimens.

It was only by means of sections that it was possible to trace the nerve in the cavity of the hair, and I found it very

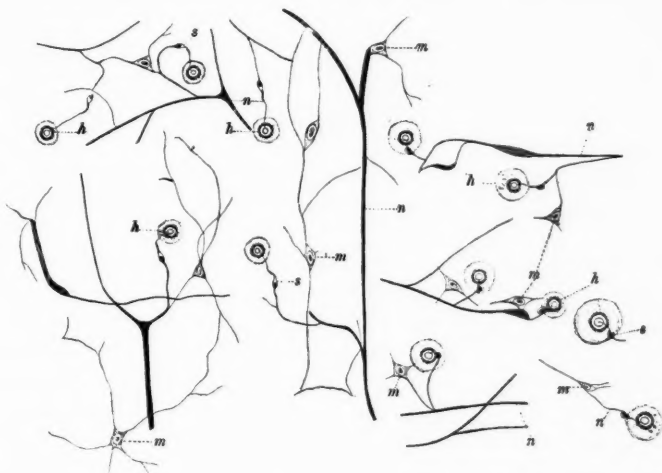


FIG. 6.—The figure in the center and those at the left are surface views of subhypodermal nerves and cells from the silkworm; the bases of the hairs are also shown. The figures at the right are the same from the myron sphinx (*Ampelophaga myron*). Methylene blue.

difficult to obtain successful preparations. In the silkworm nerves were traced to the hairs by means of sections, which showed the nerves passing between the hypodermal cells, past the gland cell, or trichogen cell, without any branches, and often as far as the collar of the hair. In a few cases the nerves were traced a short distance into the shaft; but they appeared to end not far from the base of the hair on the side of the lumen (Fig. 7). Either in the hair or just below it a rather large

swelling of the nerve was usually seen ; this is possibly an artifact. In a few cases nerves were traced perhaps one-half the length of the cavity. In these cases there was a swelling of the nerve just before its apparent termination (Fig. 7).

I found no evidence to indicate nerves ending in gland cells or trichogen cells by such branches as have been described and figured by Blanc ('90), but in every case the very fine nerve termination could be traced up past the hypodermal cell layer with no branches.

SUBHYPODERMAL NERVE PLEXUS.

Villanes ('81), in insects, figures a subhypodermal nerve plexus made up of multipolar nerve cells. In '93 Rina Monti, also working on insects, described a similar plexus, and in '95 Bethe described similar structures in Crustacea. Nemec ('96), in isopods, and Holmgren ('96), in a sphinx-moth larva, show multipolar networks of subhypodermal cells. All the work thus far was by means of methylen blue or ordinary methods, and because of the apparent antagonism with the neuron theory much attention was directed to this subepithelial plexus, and doubts were raised as to the nervous nature of these cells. In 1898 Schreiber, who had already in 1897 together with Nusbaum published a paper on the peripheral nervous system of Crustacea showing these multipolar cell plexuses, published another short paper showing these cells demonstrated by means of a modified Golgi method, and at the close of his article draws the following conclusions :

1. An identical methylen blue staining of the subepithelial multi- and bi-polar nerve cells.
2. Like staining of both forms of cells by the Golgi method.
3. True connections of the nerve cells with nerves.

A few months later Holmgren confirms, on the whole, Schreiber's results, but speaks of many-branched subhypodermal cells, as described by Bethe in Crustacea, and probably confused by Nusbaum, Schreiber, and other writers on Crustacea with multipolar nerve cells. Holmgren distinguishes

these cells from the true multipolar nerve cells of Crustacea, regarding them as many-branched mesenchymatous cells. In lepidopterous larvæ Holmgren states that there are no mesenchymatous cells like those in Crustacea which one would confuse with nerve cells.

In 1897 and 1898 Duboscq criticises the work of many previous workers upon multipolar subhypodermal nerve cells and states as his opinion that the bipolar nerve cell is the only true nerve cell in the hypodermis of arthropods, and that there is no subepithelial plexus. Although much of the criticism of a subepithelial plexus by Duboscq is very just, it seems to me that simply calling all such structures so described connective

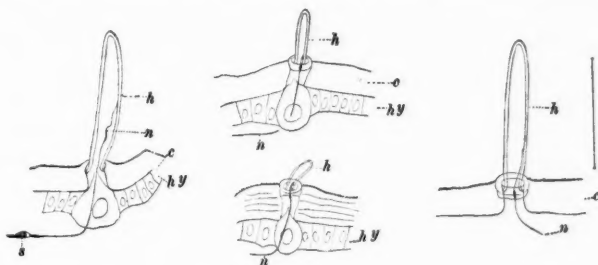


FIG. 7.—Sections through body sense hairs of the silkworm showing the nerve terminations. Methylene blue.

tissue is hardly justified when we look over the works of numerous observers. It may in part be true, as Holmgren points out, that much which has been described, especially in Crustacea, may come under the head of mesenchyma, but do we not have multipolar nerve cells as well?

The occurrence of evidently multipolar nerve cells together with bipolar nerve cells and fibers I found to be very constant in lepidopterous larvæ (Fig. 6). The nucleus of these multipolar cells was a very well marked, clear area occupying a large part of the center of the cell; in the center of this clear area was a darker staining portion, possibly the nucleolus. These cells with their many fine branches always take a paler blue stain than the other nervous structures in the skin. The very fine branches of these multipolar cells run out long

distances, and in the most successful preparations may be seen to join with similar branches from other multipolar cells and with other nerves. In some cases, as shown in Figs. 5-6, branches from these went directly to bipolar nerve cells or to large nerve trunks. These cells are always either in series with at least one bipolar nerve cell (Fig. 6) or have some of their branches joining the nerve trunk of the bipolar cell, or they are not far from one of these sensory cells. Often it was seen that these cells occupied a position closer to the hypodermal cells than other nervous tissues, and sometimes large nerve trunks would end bluntly, and under the ends of such trunks would be found a multipolar cell, perhaps giving one of its branches to a bipolar nerve cell (Fig. 6).

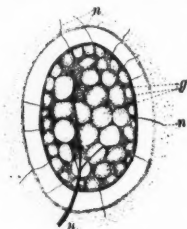


FIG. 8. — Inner face of body wall of tiger-moth larva tubercle, showing nerves going up into the elevation and breaking up among the large cells at the bases of the hairs. ($\times 22$.) Methylen blue.

These cells were best observed in the silkworm and in the myron sphinx larva, but they were also seen in *Pieris*, *Datana*, *Papilio*, and practically in all forms studied. Whether these multipolar cells are nervous tissue or not cannot be fully decided as yet, but although they differ somewhat in position and staining qualities from other undoubted nerve cells, they have many characteristics which favor their being regarded as nervous tissue.

Aside from a network of multipolar cells with their processes another sort of plexus was observed. In tiger-moth larvæ the hairs are on little knoblike elevations. After injection and staining of nerve fibers there are found to go to each of these hair tubercles a large nerve, which, after entering the elevation, may be seen to break up into branches (Fig. 8), and in sections it may be seen that these branches break up still finer and each subdivision goes to a bipolar cell connected with a hair. Now, besides these larger nerve trunks, smaller ones are also seen entering the elevations, and often in successful preparations near the edge of the hair tubercles there may be seen a very complex network of apparent nerve fibers with many swellings, as shown, much enlarged, in Fig. 9. This network

is apparently entirely without cellular elements and is at the same time a part of the nervous system. These networks in tiger-moth larvæ were only observed near the hair tubercles; in the silkworm a much less marked network of large and small fibers was occasionally found.

It is hard to say whether this network is truly a part of the nervous system or not; but in any case these networks are



FIG. 9. — Nerve plexus from edge of hair tubercle of tiger-moth larva, much enlarged.
Methylen blue.

not at all like the multipolar cells just described, no nuclei or cells being recognized, but they are well stained with methylen blue and join undoubted nerves.

CENTRAL ENDING OF SENSORY NERVES.

It was not the purpose of this investigation to make a study of the central nervous system, but as it became necessary to trace the nerve fibers to the ganglia, several interesting conditions were noticed which have a more or less direct bearing upon the previous work; a few of these will be spoken of, although it is realized that no complete discussion can be given without considerable further study, and consequently further

investigations will probably bring out more complex relations than here portrayed.

On each side of the abdominal ganglia of *Pieris* there are two large branches or nerve trunks (Fig. 10). The more cephalic of these comes from bipolar nerve cells at the bases of hairs, and the other more caudal branch goes to muscles; so, as nearly as could be determined, the cephalic trunks are sensory and the caudal ones motor. There may have been a few motor nerves in the cephalic trunk and sensory nerves in the caudal one, but if there were such, they were inconspicuous and not noted in the examination of numerous specimens; so for the present, at least, the more cephalic branch may be regarded as a sensory branch.

This sensory branch upon entering the ganglion seems to run as a distinct tract cephalad without sending branches to the central cell area of the ganglion. This tract runs cephalad for some distance along the outside of the connective and is finally lost sight of. The course of the motor nerve is quite different; its fibers seem to come

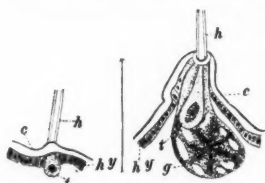


FIG. 12. — Small and large hairs from *Pieris rapa*.

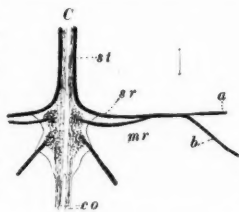


FIG. 11. — Abdominal ganglion from *Io* caterpillar (*Automeris io*). *a*, from hairs; *b*, to muscles.

directly from the central cell area of either side of the ganglion. Aside from the fibers just described, there are nerve fibers which may be seen to run through the ganglion longitudinally; these take a lighter stain. They run along the connectives and are just inside the sensory tracts.

Variations in the number and position of the nerve trunks from the ganglion occur in different species. In *Io* and in a tiger moth the same sensory tract may be noted, but part of the sensory trunk upon entering the ganglion leaves the sensory tract and enters the cell area (Fig. 11), but on

tracing the nerve to the periphery it is found that part of the fibers of the more cephalic nerve come from the muscles, and so the nerve may be regarded as a mixed nerve, showing why some of its fibers do not follow the sensory tract.

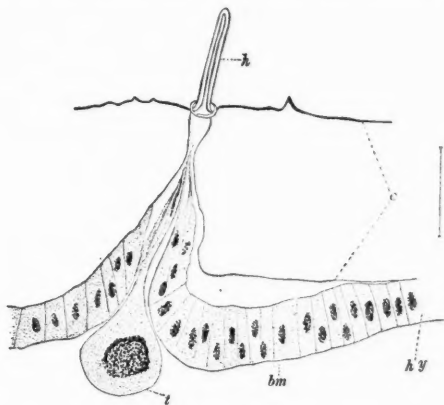


FIG. 13.—Section of hair from *Sphinx chersis*.

In lepidopterous larvæ the two sides of the ganglia seemed to be separate, possibly because of imperfect methylen blue stain. In *Coryalis* larva fibers were seen to cross from side to side.

GENERAL RESULTS.

In the lepidopterous larvæ examined two kinds of body sense hairs were found: first, *simple hairs*, those having a single enlarged hypodermal cell at the base (Fig. 12); and, second, *glandular hairs*, or those having two rather large modified hypodermal cells (Fig. 12). In the latter case the smaller cell is probably the trichogen cell, and the other a glandular cell of some sort. As these figures were drawn from specimens prepared in the ordinary way, the nerves are not shown.

Examples of simple hairs are represented by Figs. 13–18. The insects from which these figures were drawn are indicated in the explanations of the plates. Glandular hairs are represented by Figs. 12 and 19.

In all species examined both simple hairs and glandular hairs were found to be supplied with a bipolar sensory nerve cell and fiber. Sometimes, as in *Pieris* and *Datana*, there are

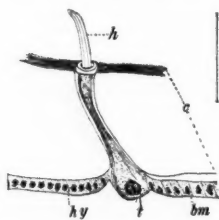


FIG. 14. — Section of hair from body surface of *Thyreus abbotti*.

two quite distinct kinds of hairs, large and small. In this case the large hairs are supplied by large bipolar nerve cells, and the small hairs by small ones (Fig. 20). In tiger moths and tussock moths the hairs differ somewhat from those in other forms; here the single hairs of other lepidopterous larvæ are represented by bunches of hairs clustered together on tubercles. Each tubercle is supplied by one or more large nerve trunks, which break up on entering the tubercle. A bipolar nerve cell from each hair in this case is harder to determine absolutely; but as some of the hairs were found to have such nervation, probably all do, for all are of the same kind. The structure of these hairs differs somewhat from those already described in the form and shape of the cells, these sometimes being hollow or saclike with radiating nuclei (Fig. 2). The base of the hairs also presents variations, as shown in Fig. 2; here the chitinous base of the hair seems to extend down below the level of the cuticle. In a section

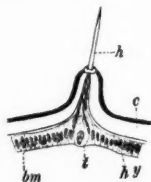


FIG. 15. — Section of hair of *Basilarchia archippus*.

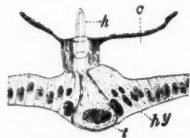


FIG. 16. — Hair from *Samia cecropia*.

through the base of a hair of *Notolophus* (Fig. 21) the opening of the hair is seen to be nearly closed in two places by strong processes of chitin, and sections taken just one side of the middle line show apparently a closed hair, indicating how small the opening is in the base of the hair.

All the hairs examined in lepidopterous larvæ were open and undoubtedly sensory, that is, supplied with bipolar sense cells.

Differing from the hairs just described, there are distributed over the surface of the body of the larva of the Io moth spine-like clusters, prolongations of the body wall (Fig. 22); most of these spines are tipped with short, strong, chitinized caps, and a few with long, slender, hairlike processes. These spines when touched to the tender surface of the hands produce swellings which are slightly painful. Numerous specimens stained by methylen blue demonstrated fine nerves running into these spinous processes and extending almost to the tips, but no bipolar nerve cells were demonstrated. Evidently here we have glandular hairs, but not sensory hairs; however, in the same specimens there were found hairs of the usual type, much smaller than these processes of the body wall or spines; these true hairs were located both on the bases of the spines and upon the body wall between the spine clusters (Fig. 22, *h*). No difficulty was experienced in demonstrating a bipolar nerve cell at the base of each of these true hairs.

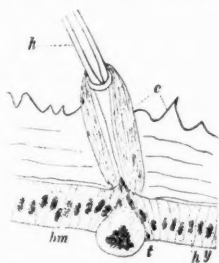


FIG. 18. — Silver-spotted skipper (*Ephargyreus tityrus*).

To summarize briefly: all lepidopterous larvæ studied have their bodies clothed with hairs, and all the hairs are sensory, having a bipolar nerve cell at their base and supplied with a minute nerve fiber, with the possible exception of the poison spines of Io caterpillars.

To carry the generalizations a little further, the following observations are useful. In the larvæ of May beetles the hairs of the body surface are supplied with bipolar nerve cells (Fig. 23), and in Orthoptera, as already spoken of by Duboscq ('97), the hairs have a bipolar sense cell at their base. In the larva of *Corydalis*, bipolar nerve cells with their fibers supply each of

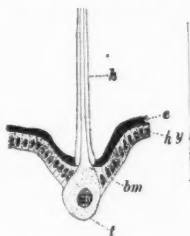


FIG. 17. — Simple hair from *Chisio-campa americana*.

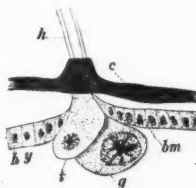


FIG. 19. — Large, probably glandular hair from *Chisio-campa*.

the numerous little, black, scalelike hairs which so thickly cover the body; large hairs have larger bipolar nerve cells (Fig. 3).

Günther ('01) shows scales of a lepidopterous wing with nerve cells at the base of both simple and glandular scales, probably a similar result to that just described in *Corydalus*.



FIG. 20.

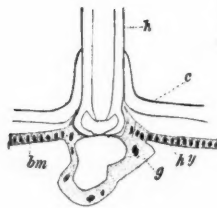


FIG. 21.

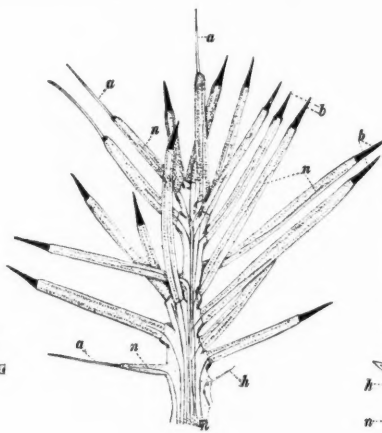


FIG. 22.



FIG. 23.

FIG. 20. — Bases of large and small hairs from *Datana*, showing their bipolar nerve cells. Methylene blue.

FIG. 21. — Section through center of hair of *Notolophus leucostigma*.

FIG. 22. — Cluster of spines from *Io*. ($\times 17$.) Methylene blue. *a*, hairlike spine; *b*, usual type of spine.

FIG. 23. — Large and small hairs from beetle larva with their sense cells and nerves. Methylene blue.

SUMMARY.

1. Lepidopterous larvæ are clothed with hollow hairs, each of which is supplied by a bipolar nerve cell, a process of which penetrates a short distance into the hair and probably terminates before reaching the tip.

2. In most species all body hairs are sensory; large hairs are supplied by large bipolar nerve cells, and small ones by smaller bipolar cells.

3. Under the hypodermis of caterpillars there is a system of multipolar cells more or less intimately connected with nerve

cells and fibers which (*a*) stain lighter than the larger nerves and (*b*) are closer to the hypodermis than the other cells and fibers.

4. Nerves from bipolar sensory nerve cells go to the central nervous system, run to the ganglia, leaving at once to follow on the outside of the connectives cephalad, forming a well-marked sensory tract. Motor nerves—those that go to muscles—seem to come directly from the central cell areas of the ganglia.

5. Almost the only sensory termination of nerves on the body of insects is by means of hairs.

I wish to make my very sincere acknowledgments to Professor Comstock and the Department of Entomology for much invaluable aid in the preparation of this paper.

BIBLIOGRAPHY.

- '96 BETHE ALB. Ein Beitrag zur Kenntniss des peripheren Nervensystems von *Asticus*. *Anat. Anz.* 1896.
- '97 BETHE ALB. Das Nervensystem von *Carcinus menas*. *Arch. f. Mikr. Anat.* 1897.
- '90 BLANC, M. L. La tête du *Bombyx mori* à l'état larvaire. Extrait du volume des travaux du laboratoire d'études de la soie. Lyons, 1889-90.
- '97 DUBOSCQ, O. Sur la terminaison des nerfs sensitifs des chilopods. *Ann. de l'Univ. de Grenoble.* 1897.
- '97 DUBOSCQ, O. Sur le système nerveux sensitif des tracheates (orthopteres, chilopods). *Arch. de Zool. Exp. et Génér.* 1897.
- '98 DUBOSCQ, O. Recherches sur les chilopods. *Arch. de Zool. Exp. et Génér.* Sér. 9, tome vi. 1898.
- '01 GÜNTHER, K. Ueber Nervenendigungen auf dem Schmetterlingsflügel. *Zoöl. Jahrb.* Bd. xiv. 1 Taf. 1901.
- '80 HAUSER, G. Physiologische und histologische Untersuchungen über das Geruchsorgan der Insecten.
- '95 HOLMGREN, E. Studier öfver hudens och koertebart hudorg. morfolog. hos skand. mikrolepidopterlarven. *K. Svenska Vetensk.-Akad. Handlingar.* 1895.
- '95 HOLMGREN, E. Zur Kenntniss des Hautnervensystems der Artropoden. *Anat. Anz.* 1895.

- '93 HOLMGREN, E. Zum Aufsätze W. Schreibers "Noch ein Wort." *Anat. Anz.* 1898.
- '81 KUNCKEL et GAJAGNAIRE. Rapport du cylindre-axe et des cellules nerveuses périphériques avec les organes des sens chez les insectes. *C. R. Acad. Sc.* 1881.
- '51 LEYDIG, F. Anatomisches über Corethra plumicomis. *Zeitschr. f. wiss. Zool.* 1851.
- '93 MONTI, RINA. Ricesche microscopiche sul sistema nervoso degli insetti. *Boll. scient.* 1893-94.
- '96 NEMEC, BOHUMIL. Zur Kenntniss des peripheren Nervensystems einiger Crustaceen. *Anat. Anz.* 1896.
- '97 NUSBAUM and SCHREIBER. Beitrag zur Kenntniss des peripherischen Nervensystems bei den Crustaceen. *Biol. Centralbl.* 1897.
- '91 RATH, O. VOM. Zur Kenntniss der Hautsinnesorgane der Crustaceen. *Zool. Anz.* 1891.
- '92 RATH, O. VOM. Ueber die von C. Claus beschriebene Nervenendigungen in den Sinneshaaren der Crustaceen. *Zool. Anz.* 1892.
- '94 RATH, O. VOM. Ueber die Nervenendigungen der Hautsinnesorgane der Arthropoden nach Behandlung mit der Methylenblau und Chromsilbermethode. *Berichte der natur. Gesellsch. zu Freiburg.* 1894.
- '96 RATH, O. VOM. Zur Kenntniss der Hautsinnesorgane des sensiblen Nervensystems der Arthropoden. *Zeitschr. f. wiss. Zool.* 1896.
- '90 RETZIUS, G. Zur Kenntniss des Nervensystems der Crustaceen. *Biol. Unt.* N.F. 1896.
- '92 RETZIUS, G. Ueber die Nerven-Prinzipien in der Lehre von der Einrichtung des sensiblen Nervensystems. *Biol. Unt.* N.F. 1892.
- '95 RETZIUS, G. Das sensible Nervensystem der Crustaceen. *Biol. Unt.* N.F. 1895.
- '98 SCHREIBER, W. Noch ein Wort über das peripherische sensible Nervensystem bei den Crustaceen. *Anat. Anz.* 1898.
- '81 VILLANES. Sur les terminations nerveuses sensibles dans la peau de quelques insectes. *C. R. Acad. Sc.*
- '83 VILLANES. Recherches sur l'histologie des insectes et sur les phénomènes histologiques qui accompagnent le développement postembryonnaire de ces animaux. *Th. Paris.* 1883.

 ABBREVIATIONS USED IN FIGURES.

<i>bm</i> = basement membrane.	<i>h</i> = hair.	<i>co</i> = connective.
<i>C</i> = cephalic direction.	<i>hy</i> = hypodermis.	<i>m</i> = multipolar cell.
<i>c</i> = cuticle and cuticular thickenings.	<i>mr</i> = motor root.	<i>n</i> = nerve.
<i>ca</i> = central cell area.	<i>s</i> = sensory cell.	<i>sr</i> = sensory root.
<i>g</i> = gland cell.	<i>st</i> = sensory tract.	<i>t</i> = trichogen cell.
Lines near drawings indicate $\frac{1}{10}$ mm.		

HISTOLOGICAL CHANGES IN HYDRA VIRIDIS DURING REGENERATION.

HANNAH TERESA ROWLEY.

ALTHOUGH a great deal of work has been done on the regeneration of hydra, no one has as yet attempted to make out the histological changes that take place. This point would seem to be one of special interest, since the old piece appears to change its form as a whole to produce a new animal. The principal question to which I wished to find an answer was whether, during the period of regeneration, the old cells go over without change into the tissue of the new animal, or whether new cells are formed, and if so, in what part or parts.

Green hydras were used almost exclusively, since they regenerate more readily and with fewer abnormalities than does the brown species. Hydras of various lengths were taken, the foot end and circle of tentacles were cut away, and the remaining middle parts of the body wall were each divided by cross cuts into four—in some cases two—small rings. These were allowed to regenerate, and at different periods, ranging from immediately after the cutting to some days after the formation of new tentacles and foot, were killed in a solution of corrosive acetic, hardened, sectioned lengthwise, and stained in Delafield hæmatoxylin. In some cases the slides were dipped for a moment into a weak solution of picric acid in absolute alcohol, in order to differentiate the endodermal tissue.

Observation of the living piece showed that the ends became rounded, closing in from fifteen to sixty minutes after having been cut; that the piece then remained without permanent change of form for thirty or forty hours, although at intervals it might change its shape by expanding and contracting. At about this time small knoblike outgrowths, the tentacles, began to appear at one end, the other end fixed itself to the nearest

support, and in a few days the proportions of a normal hydra were assumed.

Serious difficulties arose in the microscopic study of the prepared sections, which it may be well to mention. Although undoubted karyokinetic divisions were seen in both neuro-muscular and interstitial cells of the ectoderm, and in the endoderm, it was found almost impossible to determine the exact amount of dividing tissue, for the following reasons.

Throughout the entire period of regeneration there is an active production of new nettle cells, which are formed from interstitial cells of the ectoderm. This process begins by a slight sickle- or moon-shaped thickening of protoplasm along a part of the cell wall. In certain sections this thickening appears as a small, darkly stained rod which may easily be mistaken for a small nucleus in process of division. Again, in sectioning, this curved, thickened rod may be cut at such an angle as to bring distinctly into view only its extremities, producing the appearance of two small groups of darkly stained material. These could be distinguished from two separating groups of chromosomes only by bringing into focus the connecting line of the rod, which would lie slightly above or below the ends. In many cases it was found almost impossible to determine whether such a cell was forming a cnidocyst or was dividing karyokinetically. These difficulties were increased by the small size of many of the interstitial cells, by the fact that the wall of such cells is not sharply defined, and by the fact that at the time of the formation of nettle cells it is very often difficult to make out the nuclei of the changing cells.

Moreover, many nuclei of both neuro-muscular and interstitial cells were found to be in a state that distinctly suggested activity of some sort, — the chromatin mass large and loose, or even in many interstitial cells broken and scattered throughout the nucleus. This appearance was very different from that of nuclei of typical resting cells in the same section, the latter containing one or two well-defined nucleoli. Yet the large number of nuclei with the chromatin scattered as just described, in sections containing comparatively few karyokinetic spindles, would seem to indicate that all such cells were not necessarily

dividing. Where so many cells were about to divide or had just completed division, we should expect to find a corresponding number undergoing the actual process. This, however, was not the case.

A further point should also be kept in mind, *viz.*, the possibility that multiplication of the interstitial cells may be concerned with the development of new nematocyst cells rather than with the regeneration of new tissue.

In order to get more light on these points, the tissue of a normal hydra was examined for comparison with that of the regenerating piece. Another hydra was irritated with a blunt needle in order to induce it to discharge the nettle batteries. It was then left undisturbed for about twenty hours, at which time it was killed and the tissue prepared as has been described. It was hoped by these means to obtain further light on the difficulties of the question, and to be able to distinguish more clearly between the phenomena of regeneration and those merely incidental to the formation of new nettle cells.

In the case of the stimulated hydra, nettle cells were found to be forming as in the regenerating pieces. Moreover, in the tissue of this hydra and of the undisturbed normal one also I was surprised to find undoubted evidence of cell division, in addition to the very general loose and broken appearance of the chromatin in some of the interstitial cells, which has been noted as occurring in the regenerating piece. This latter condition, found in a hydra upon which no operation had been performed, made it still less possible to consider such nuclei as dividing. On the other hand, a piece that had been regenerating seven days, and that had attained to the proportions of a normal polyp, was found to present the same appearance under the microscope. It is possible, therefore, that the normal tissue examined was that of a growing hydra, and that these conditions are common to the regenerating and growing forms, while further examination of the tissue of fully grown hydras might show a somewhat different state.

While these latter experiments, therefore, threw little light on the amount of division in the regenerating piece, yet the similarity in appearance between this regenerating tissue, the

tissue of the regenerating piece after the normal form had been attained, and the tissue of normal or growing hydra is of importance in a consideration of regeneration in this form.

I shall now attempt to make a conservative statement of the amount of dividing tissue in regenerating hydra, based on undoubted cell division.

There is very little evidence of the formation of new tissue during the early stages; an exception was noted in one piece killed five hours after the cutting, in which a number of divisions were observed in the ectoderm. Some few divisions can be observed before twenty hours, but from forty hours on, — the time of tentacle formation, — the division is more active and the number of dividing cells, especially neuro-muscular cells, is considerable. Division continues after the tentacles have begun. Spindles were seen in endodermal cells, and in neuro-muscular and interstitial cells. These divisions often occur in groups, especially in the neuro-muscular cells. In one case as many as five dividing nuclei of neuro-muscular cells were observed at one spot in a section cut from the side of the piece and so affording a surface view of ectoderm tissue alone. Fewer divisions were seen in the endoderm than in the ectoderm, partly, perhaps, because of the smaller number of cells in the endoderm.

Unlike the majority of cases of regeneration, however, the new cells are not formed at the cut surface alone, and the tentacles do not seem to be regenerated solely from new tissue. Divisions were found to occur as well at the sides as at the ends of the regenerating pieces, and in almost, if not quite, as great number. The first appearance of the tentacle, which in the living animal seems to be brought about by an outpushing of the tissue of the original piece, appeared under the microscope to be due very often to contraction in this region, causing a very slight protuberance of ectoderm, which could be fully accounted for by an outpushing of old material without the formation of new tissue. Divisions were sometimes seen at this place, sometimes not. Very frequently, however, in later stages, when the tentacle had grown to some length, there was seen to be a group of neuro-muscular cells dividing

at the base of the tentacle, and interstitial cells were seen to be dividing quite rapidly in the tentacle itself. It would seem, on the whole, that new tissue is furnished to the tentacle by division of cells at the proximal end, or base, rather than by division of cells that have already entered into the new organ.

With the exception of the formation of nettle cells from interstitial cells, it is not found that cells of one kind give rise to cells of another, but that neuro-muscular cells of the new hydra result from neuro-muscular cells of the piece, and interstitial from interstitial.

Considering, therefore, that the first appearance of the tentacle may be unaccompanied by cell division in its immediate neighborhood; that cell division, though frequently found in the region of the growing tentacle, is not confined to this region but is found elsewhere throughout the length of the regenerating piece; that division is found to be present as late as seven days after the cutting, that is, after the piece has assumed the proportions of a normal hydra; and that some division is observed in the tissue of the normal, probably rapidly growing hydra, — we are justified, I think, in concluding that the new cells which appear during the regeneration of hydra are formed by division of the old cells throughout the entire piece, as in the normally growing animal, and that the tentacles are formed from old cells and from cells that have arisen by division of the already differentiated cells of the old part.

I am very much indebted to Prof. T. H. Morgan, under whose direction this work was carried on.

BRYN MAWR, January, 1902.

NOTES AND LITERATURE.

ZOÖLOGY.

The Fishes of Guam.—In the director's report of the Bernice Pauahi Bishop Museum at Honolulu (for 1900), Mr. Alvin Seale, curator of fishes, gives a record of the birds and fishes collected by him on the island of Guam. Two hundred and seventy-four species of fishes were obtained, of which eighteen are described as new, useful descriptions being given of all the others. The fauna differs considerably from that of Hawaii, the number of species common to the two groups of islands being less than one-third of the number enumerated. The fauna of Guam naturally approaches more nearly to that of the East Indies. In commenting on this most valuable and helpful piece of work, the first accurate faunal list of fishes of Polynesia yet published, two minor criticisms are necessary.

The proof reading should receive more careful attention; *Zebra-soma* appears three times as *Zabrasoma*, and *Garres argyus* stands for *Gerres argyreus*. Still more important is the form given to new names. *Pseudoscarus platodoni* apparently refers to the broad teeth (platyodon or platyodus). *Percis cephalopunctatus* is unfortunately named and is, of course, not an agonoid, but a species of *Parapercis*, a genus of trachinoid affinities. *Gobius deltoides* belongs to some genus other than *Gobius*. These and other corrections will doubtless be made in due time by the author, and the work will prove most useful to future students of the Polynesian fish fauna. D. S. J.

Notes on Fishes.—Henry W. Fowler notes in the *Proceedings of the Academy* at Philadelphia (Vol. LIII, Pt. III) the occurrence of *Myctophum phengodes*, collected off the west coast of Greenland by Dr. Hayes.

In the *Zoologischer Anzeiger* (Bd. XXV, No. 666) Dr. Poche calls attention to the identity of the three nominal genera of siluroid fishes, called *Amphilius*, *Anoplopterus*, and *Chimarrhoglanis*, the name *Amphilius* being the earliest.

In the records of the Australian Museum, Edgar L. Waite records numerous fishes from western Australia, with valuable notes and

several plates. In another article he gives useful notes on an Australian shark, *Galeus*, or *Mustelus antarcticus*, and its peculiar placenta-like structure attached to its young.

In the *Zoologischer Anzeiger* for Nov. 25, 1901, Dr. K. Kishinouye, head of the Fisheries Bureau of Japan, describes a new shark, *Rhinodon pentalineatus*, taken off Cape Inubo in Japan. This huge animal is over thirty feet in length, and had an oak stick a foot long in its stomach. The stuffed skin is preserved in Tokyo.

A skin of the whale shark called *Rhinodon typicus* has just been received at the United States National Museum from Ormond, Fla. The skin is eighteen feet long. The species is known thus far from the type from the Cape of Good Hope and from teeth taken at the Seychelles Islands. Mr. B. A. Bean notes this discovery in *Science*.

In the *Bulletin de la Société Philomathique* (N.S., Tome III, Nos. 3, 4) Dr. Pellegrin discusses those fishes which develop with age an adipose pad on the forehead. This is found in numerous wrasse-fishes, parrot fishes, snappers, and others. These appendages are chiefly confined to adult male fishes and are made of adipose tissue. Pellegrin compares it to the deposit of fat in old age in some human individuals.

In the *Overland Monthly* for February and March Mr. Cloudsley Rutter of the United States Fish Commission gives the story of the Sacramento salmon in very unique fashion. A full account is given of each detail in the life history of the fish, together with photographs of scenes and places on the salmon's route, and a very large number of illustrative drawings. Among the fantastic stories of animals now in vogue, many of them having no existence in real nature as distinguished from the forests of Kiplingia, it is refreshing to find a fish story, at once natural and true, the result of years of patient observation.

In the *Proceedings of the United States National Museum* (Vol. XXIV, Nos. 1260, 1261, and 1263) Jordan and Snyder continue their monographic reviews of Japanese fishes, treating the various forms combined by Günther under the head of Trachinidæ. They follow Boulenger in separating from this group all the species with thoracic ventrals as being percoid rather than trachinoid in their affinities. Twenty-six species are enumerated, seven being new. Three new genera, *Pteropsaron*, *Ariscopos*, and *Stalix*, are described and figured. Of the *Discoboli*, four species are enumerated, *Lethotremus awae* and *Crystallias matsushimæ* being new, the latter the type of a new

genus near *Liparis*. The Embiotocidae, or surf fishes, consist of two species in Japan, *Ditrema temminckii* and *Neoditrema ransonneti*. The Pediculati, or angler fishes, of Japan consist of eleven species, the following being new: *Antennarius nox*, *A. scriptissimus*, *A. sanguifluus*, *Malthopsis tiarella*. The last two papers are by Dr. Jordan, assisted by a Japanese student of fishes, Michitaro Sindo.

Mr. William H. Gregg has published a convenient volume on *When, Where, and How to catch Fish on the East Coast of Florida*. The greater part of the book is devoted to a systematic account of the game fishes of the east coast of Florida, with numerous figures taken from government publications. The systematic part is arranged from the writings of Jordan and Evermann, which is very proper when credit is given, as Mr. Gregg has been careful to do. To make popular works of this sort possible is one of the duties of the systematist. After describing the fishes Mr. Gregg tells in an accurate and readable fashion how and when to catch them.

In the *Annals and Magazine of Natural History* (Vol. IX, No. 51), Dr. G. A. Boulenger discusses the classification of the berycoid fishes. He finds that this group differs from the percoids in no important respect, and regards the berycoids as merely archaic percoids. The chief diagnostic character, the increased number of ventral rays, is found in most berycoids. Pempheris, however, differs from Beryx almost solely in having the usual number of ventral rays, I, 5, found in most spiny-rayed fishes. Zeus and Grammicolepis, perhaps not related to Beryx, have also an increased number. Aphredoderus is placed among the berycoids by Boulenger. The resemblance of the fossil genus *Asineops* to the Berycidae is also noted, while *Erismatopterus* is thought to have no near affinity. To the present writer *Erismatopterus* resembles the Percopsidae, having much in common with *Columbia*. Boulenger rightly separates Pempheris from the Kurtidae, and he suggests the close relationship of both Pempheris and *Bathylupea* to Beryx. *Stephanoberyx* and *Malacosarcus* he would place among the Haplomi. *Polymixia* he regards as an ally of Beryx, and *Morocentris* as a more distant relative. *Hoplostethus* he unites with *Trachichthys*, while a new genus, *Gephyroberyx*, is proposed for *Trachichthys darwini*. The genus *Paratrachichthys* with the vent advanced is rightly regarded as valid.

D. S. J.

Twenty New Pocket Mice. — Pocket mice are mice with pockets, not mice intended to be kept in the pocket, as the reader may innocently suppose. Dr. C. H. Merriam (*Proc. Biol. Soc. Washington*,

March 5, 1902) has given us a most important contribution to the knowledge of these animals, principally based on the material (some 800 specimens) collected by Messrs. Nelson and Goldman in Mexico. The genus *Heteromys* takes the place of our common *Perognathus* in the warmer parts of Mexico and in Central America, but comes north (as Dr. Merriam's paper shows) into the states of Chihuahua and Sonora, and to Brownsville, Texas. However, these more northern animals, along with a number of others, represent a type so far departing from typical *Heteromys* that Dr. Merriam segregates them under a new generic name, *Liomys*. The type of the new genus is *Liomys alleni*, — the *Heteromys alleni* of Coues, 1881.

Taking *Heteromys* and *Liomys* together, and considering only the fauna of America north of Panama, no species were known previous to 1868, when Gray described four. In 1874 Peters described one, in 1881 Coues one, in 1893 Thomas published four, and two were made known by Allen and Chapman in 1897. Thus, in all, twelve were known; and to these Dr. Merriam now adds twenty!

T. D. A. C.

Osteology of the Flamingoes. — Dr. R. W. Shufeldt¹ describes the skeleton of the flamingo (*Phenicopterus ruber*) with special reference to the relations of the flamingoes to the Anseres (ducks, geese, swans) on the one hand, and to the Herodiones (ibises, herons, storks) on the other. The author compares minutely the flamingo skeleton, bone by bone, with the skeletons of representatives of the other groups. On the whole, the flamingo skeleton presents a mixture of anserine and ibidine characters, together with certain characters which are distinctly peculiar to itself. For the most part there is no marked predominance of either anserine or ibidine features. In furcula, coracoid, and wing skeleton, the anserine characters are in excess. The tarso-metatarsus resembles most closely that of an ibis.

The author concludes that, so far as the skeleton is concerned, the flamingoes should constitute an independent group or suborder (Odontoglossæ, corresponding to Huxley's Amphimorphæ) standing between the anserine and pelargo-ibidine forms.

H. W. R.

Regeneration in *Hydra viridis*. — *Hydra viridis* has been made the subject of a series of regenerating and grafting experiments by

¹ Shufeldt, R. W. Osteology of the Flamingoes, *Annals of the Carnegie Museum*, vol. i (1901), pp. 295-324, Pls. IX-XIV.

Dr. Helen Dean King.¹ It was found that the removal of the oral end by a cut just below the tentacles was followed by the regeneration of fewer tentacles than were possessed originally, while the diameter of the regenerated hypostome was less than that of the original hypostome. As this operation reduces the volume of the body, the result appears to agree with the view advanced by Parke² (p. 702), "that a certain ratio exists between the size of a Hydra and its number of tentacles, and that when this ratio is destroyed by an increase or decrease in size of the Hydra, there will be an increase or decrease in the number of tentacles of that Hydra." When the tentacles were removed by cutting at the base of each one so as not to diminish the volume of the trunk, in most cases as many tentacles were regenerated as had been removed.

The severed "heads" remodeled themselves into small polyps, and, although the hypostomes suffered reduction in diameter, in no case was a reduction in the number of tentacles observed, in spite of the smallness of the polyps. This, the author maintains, does not support Parke's view. (It should be noted, however, that Parke's statement was made with reference only to change of size resulting from favorable or unfavorable conditions, — not to decrease in volume by the mechanical removal of part of the body.)

Double-headed forms were produced by splitting the oral end longitudinally. When the tentacles were first removed, the total number of tentacles ultimately borne by the two heads together was an average of 3.4 tentacles per hydra greater than the number originally borne. When the tentacles were not removed previous to the splitting of the oral end, the average number of new tentacles developed by the two heads together was 5.1 per hydra. These double-headed polyps resolve themselves into two polyps by what resembles a process of longitudinal division, the final separation occurring at the extreme aboral end. Some of these double-headed forms were made to attach themselves oral end downwards. The separation of the two parts occurred at the aboral (upper) end as before, proving that the longitudinal fission is not due simply to the constant strain exerted by gravity at the point of divergence of the two branches of the trunk.

¹ King, Helen Dean. Observations and Experiments on Regeneration in *Hydra viridis*, *Arch. für Entwicklungsmech. der Organismen*, Bd. xiii, Hefte 1 and 2 (1901), pp. 135-178. 31 text-figs.

² Parke, H. H. Variation and Regulation of Abnormalities in *Hydra*, *Arch. für Entwicklungsmech. der Organismen*, Bd. x, Heft 4 (1900), pp. 692-710. 9 text-figs.

If the cut edges of a split oral end are permitted to reunite, new tentacles develop at the regions of union. Polyps with fourteen tentacles were thus produced, but the repetition of the operation on a fourteen-tentacled hydra resulted in no further increase of tentacles.

Attempts were made to secure heteromorphosis, or reversal of "polarity," by grafting. In several cases tentacles were developed upon an aboral cut surface or a foot upon an oral cut surface, but in all these cases (which the author interprets as heteromorphosis) the pieces whose polarity appeared to be reversed were very small parts of the trunk. In the case of a graft of any considerable length, the free cut end reproduced parts similar to those which had been cut away from it. In the cases of apparent heteromorphosis exhibited by very small fragments of the trunk, can it be proved that there is not a shifting about of the tissues or a migration of cells, so that the regeneration does not really involve a reversal of polarity?

H. W. R.

A Revised Classification of the Enteropneusta.—It is nine years since Spengel's great monograph of this group was published.

A number of important additions to our knowledge have been made in the meantime, and the author now returns to the subject¹ for the purpose of recasting the systematic arrangement of the species, and rectifying certain violations of nomenclature which the monograph contained.

The total number of species has been increased by thirteen, and information about one of the old species, *viz.*, *Ptychodera flava* Eschscholtz, has been largely extended since the publication of the monograph.

A total of twenty-nine species is now recognized by the author. The arrangement of these into families and genera is as follows:

FAMILY I. HARRIMANIIDÆ SPENGL, 1901.

- Genus 1. *Harrimania* Ritter, 1900.
" 2. *Dolichoglossus* Spengel, 1893.
" 3. *Stereobalanus* Spengel, 1901.

FAMILY II. GLANDICIPITIDÆ SPENGL, 1901.

- Genus 1. *Glandiceps* Spengel, 1901.
" 2. *Spengelia* Willey, 1898.
" 3. *Schizocardium* Spengel, 1891.

¹ Die Benennung der Enteropneusten-Gattungen, *Zool. Jahrbuch*, Abth. für Systematik, Geographie, und Biologie der Thiere, Bd. xv, Heft 2, 1901.

FAMILY III. PTYCHODERIDÆ SPENGEL, 1893.

Genus 1. *Glossobalanus* Spengel, 1901." 2. *Balanoglossus* Delle Chiaje, 1929." 3. *Ptychodera* Eschscholtz, 1825.

The classification adopted by the author in his monograph was unfortunate in that it conflicted at several points with established rules of nomenclature. For example, the type species of *Ptychodera*, *P. flava* Eschscholtz, 1825, would have been removed by Spengel to a new genus, *Tauroglossus*. Delle Chiaje's well-known species, *Balanoglossus clavigerus*, was likewise deprived of its original generic name and placed in the suggested genus *Tauroglossus*.

Both these pioneer species are now restored to their rightful places as types of the genera to which they were originally assigned.

This latest scheme of classification of the Enteropneusta undoubtedly corresponds nearer to the actual relationship of the species than any other that has been proposed.

As the author remarks, however, the three genera constituting the Harrimaniidae are certainly considerably less closely related than are those constituting the other two families.

Dolichoglossus in particular, I would remark, is much less close of kin to the other genera of the family than these genera are to each other.

WM. E. RITTER.

Hymenoptera Parasitica Hawaiiensis. — The part of the *Fauna Hawaiiensis* (Vol. I, Part III) dealing with the parasitic Hymenoptera has just come to hand. It is written by Mr. W. H. Ashmead, who has prefaced to the purely descriptive part some very interesting remarks on the Hymenoptera of the Hawaiian group. Of the 128 parasitica enumerated, no less than 87 are described as new; these do not include any which cannot be referred to known families, but eleven genera appear to be endemic. Several of the previously known species are easily recognized as introductions from other parts of the world. Mr. Ashmead suggests that the list as given must quite inadequately represent the actual fauna, "since many of the common parasitic families, which must surely occur, are entirely unrepresented." Since writing these words, Mr. Ashmead has himself visited the islands, and no doubt he will shortly publish the results of his own collecting; but it may be pointed out that the condition observed is characteristic of oceanic islands in general, and of the Hawaiian Islands in particular, as may be seen by reference to Wallace's *Island Life*, second edition, Chapter XV. Hence,

if the missing families turn up, we may subject their representatives to close scrutiny in respect to their actual origin upon the islands. The Coccidæ of the Hawaiian Islands are quite numerous, and some have been first described from Hawaii; but evidence has now accumulated which renders it extremely probable that all the species reported have been introduced by man, and I am very much inclined to doubt the existence of a single endemic Hawaiian Coccid. Probably the same may be said of the Hawaiian ants, which are all of well-known continental genera. The bees of the islands (excluding the honey-bee) belong to only three genera, and it is interesting to note that these are all borers in the trunks or stems of plants. The bees which burrow in the ground are wholly absent.

T. D. A. C.

The Slugs of Borneo.—The naked land-mollusca of Borneo have been made the subject of an interesting paper by Mr. W. E. Collinge (*Trans. Royal Soc. Edinburgh*, Vol. XL, Part II, No. 15). The species known from the island, twenty-seven in all, are enumerated, two genera (*Wiegmannia* and *Isselentia*) and nine species being described as new. The type species of *Wiegmannia* (a genus of four species) is not stated; we may designate as such *W. gigas*, Collinge, which is the largest species; for although *W. dubia* (Wgm.) was the first described, it was not examined by the author of the genus.

T. D. A. C.

BOTANY.

Meier's "Herbarium and Plant Description"¹ is a portfolio containing twenty-five sheets folded to $11 \times 8\frac{1}{2}$ inches, one inside page being blank for the attachment of a dried specimen, and the other ruled and spaced for a description of the various organs of the plant, drawings, and other notes. On the front cover inside are concise directions for collecting, pressing, and mounting, and at the back is a ruled page for indexing the collection. The whole forms a simple arrangement meeting the usual requirements for pupil's herbariums and for such meager descriptions as are too often deemed sufficient in school work. It has the advantage, however, over many similar schemes for recording plant analyses, that ample space is afforded by the outside pages of each folder for additional notes.

F. L. S.

¹ Meier, W. H. D., Superintendent of Schools, Griggsville, Ill. *Herbarium and Plant Description*. Boston, Ginn & Company.

Leavitt's "Outlines of Botany"¹ follows substantially the general sequence of topics in Gray's *Lessons*, and retains much of what must always be highly valuable in that classic text-book. At the same time so many modifications and additions have been required to meet the needs of high schools to-day that a really new book is the result, and one that is fresh and modern in treatment, broad in scope, yet wisely restricted to parts of the subject appropriate for beginners.

The most radical departure is in the laboratory studies, which in important ways improve upon previous attempts to solve the same pedagogical problems. Instead of being frequent interruptions to the text they are kept in sections by themselves, each preceding the section of text to which it relates. They consist of explicit directions and skillfully worded questions leading the student to intelligent observation of readily obtainable material and to instructive experimentation. In addition to these aids to laboratory work many helpful suggestions to teachers are given in an appendix, while a number of good references for supplementary reading are included for the benefit of both teacher and pupil.

In the text ecological considerations play an effective though subordinate part in accounting for peculiarities in the form and behavior of organs. Primarily, however, the study of the parts of plants is firmly grounded upon their morphology. A considerable number of new figures, all of high excellence, supplement or replace those of the *Lessons*.

The work is sure to be heartily welcomed by a large number of teachers, whether among those who are struggling to make the best of meager equipment and much restricted time, or among those who are more fortunate in their opportunities. Those who use the book cannot fail to be impressed by the fine scientific spirit which animates every page.

F. L. SARGENT.

Garden Beans.²— Few attempts have been made to monograph the garden beans. The work of von Martens, *Die Gartenbohnen*, in 1860 seems to have been the only previous effort in this direction.

¹ Leavitt, Robert Greenleaf, A.M., of the Ames Botanical Laboratory. *Outlines of Botany*, for the High School Laboratory and Classroom (based on Gray's *Lessons in Botany*). Prepared at the request of the Botanical Department of Harvard University. New York, American Book Company. 12mo, 372 pp., 384 figs.

² Irish, H. C. Garden Beans cultivated as Esculents, *Report Missouri Botanical Garden*, vol. xii, pp. 81-165, Pls. XXXVIII-XLVII.

Since that time the varieties of garden beans have greatly increased in Europe and the United States. All of the leading varieties of America and Europe were cultivated at the Missouri Botanical Garden, so that the growth and seed characters were used in the descriptions. The garden beans are grouped under the following genera: *Phaseolus*, *Dolichos*, *Vigna*, *Glycine*, and *Vicia*. The author gives a short account of the origin, uses, methods of culture, with a brief account of *Bruchus obsoletus* and *Colletotrichum lagenarium*, *Uromyces phaseoli*, and *Phytophthora phaseoli*. Three species of the genus *Phaseolus* are described, *P. lunatus*, *P. vulgaris*, and *P. multiflorus*. The greatest number of varieties are listed under *P. vulgaris*. *Dolichos* is represented by *D. lablab* and *D. sesquipedalis*; *Vigna* is represented by *V. catjang*; *Glycine* by *G. hispida*, of which five garden varieties are listed, but this does not by any means comprise all of the varieties, as they are numerous in Japan and China, where the species has long been cultivated. The genus *Vicia* is represented by a single species, *V. faba*.

An excellent feature of the paper is the full citation of the literature of the genus as well as that of the species, no pains having been spared to verify references. The half-tone plates accompanying the paper greatly aid in the botanical study of the garden beans. The excellent keys for garden varieties also help to facilitate the determination of the garden forms. This is one of the most important contributions to horticultural literature in this country. In point of thoroughness it is like his paper on *Capsicum* published a few years ago in one of the earlier reports of the Garden. It is a model of excellence in every way, and it may well serve as a guide for much of the erratic work carried on in this country in listing varieties and describing the same.

The work carried out by the author is one that has long been neglected in this country. Mr. Irish is fortunate in having had at his disposal not only a large amount of material,—and such work can only be undertaken where this is at hand,—but also a good reference library, combined with acute judgment in discriminating between the puzzling garden forms.

L. H. PAMMEL.

Pfeffer's Plant Physiology.—Pfeffer's¹ revision of his *Pflanzenphysiologie* has been so thorough and so time-consuming that only the

¹ Pfeffer, W. *Pflanzenphysiologie. Handbuch der Lehre vom Stoffwechsel und Kraftwechsel in der Pflanze*. 2. Auflage. Leipzig, Engelmann, 1901. Bd. ii. 1. Hälfte.

first half of Vol. II has been made ready for publication. This first part appeared last summer. The first volume, reviewed in this journal (Vol. XXXII, pp. 450, 451, 1898), treated the subjects comprehended under metabolism. The first half of the second volume discusses growth and the factors that control it, development, variation, and inheritance — in short, different kinds of work done by the plant, dependent upon and made possible by the processes discussed in the earlier volume. In a book planned as this is, with the first volume devoted to the transformation of matter and the second to the transformation of energy, more or less repetition is necessary, but it is a repetition which gives to Pfeffer's treatment of the subjects in plant physiology the exhaustiveness which the physiologist needs. This is no book to be put into the hands of undergraduates; it is for the man who has studied long and is studying hard. However much one may wish that Pfeffer's literary style were not so difficult, one cannot help recognizing that it is full of meaning.

The arrangement of matter in Vol. II of the second edition differs somewhat from the first edition; consequently comparison of the two editions as to size is difficult. One sees at once, however, that if the second half of the volume is to treat the subjects of movements and the production of heat, light, and electricity in anything like proportional fullness, the book will be considerably larger than in the first edition. The additions to the first part are many of them the results of Pfeffer's own work, either investigation or teaching. This will be equally true of the second part of the volume.

Such a work as this, presenting the status of a science as a whole, shows where the great gaps in our knowledge are. For instance the plant physiology of to-day consists of the facts discovered in studying land and fresh-water plants, and of the interpretations of these facts. Indeed, the fresh-water algæ have taken only a minor place as subjects of physiological inquiry, so that we have to-day a physiology interpreted by too many in terms applicable to land plants only. The laboratory guides carry this to the extreme, but they show how one-sided our knowledge is. Pfeffer's book can contain only a few references to the marine algæ. I am convinced that the careful physiological study of marine plants, though such study may reveal no new principles, will modify and correct many of the conceptions prevailing to-day. The status of the science is satisfactory, but there is room for much more research.

G. J. P.

Trees in Winter.— Every observer knows that there are other ways of recognizing animals and plants than those given by the books, and we all welcome every addition to the literature of these occult ways of coming into touch with nature. That trees may, in general, be recognized as certainly in winter as at other seasons has long been known, and little handbooks codifying their winter characters have appeared in most European countries, and similar keys, etc., have appeared several times in our own country, but unfortunately usually in transient pamphlet form.

There is now published a neat and accurate little book¹ dealing with the more obviously marked deciduous trees of northeastern America, the characteristic traits of which are shown by habit half-tones, and the twig details by three-color plates. Professor Sargent stands as godfather to the book, which will be an ornament to any center table, and should do much to give incentive to those walks in winter that the few enjoy so keenly and the many forego because they lack a direct object.

T.

Notes.— Vol. V of the *Annuaire du Conservatoire et du Jardin Botanique de Genève* contains M. Briquet's administrative report; a paper by him on the flora of the mountains of Corsica; an enumeration by Hochreutiner of Malvaceæ collected by Chevalier in central Africa; a paper by Wettstein on *Gentiana* and *Euphrasia*; a revision of *Urena* by Hochreutiner; a paper by Briquet on Alpine *Hieracia*; notes on *Malope* and *Palaua* by Hochreutiner; a description of *Poa balfourii*, from the Alps, by Briquet; studies of some American Nyctaginaceæ by Heimerl; and an exchange seed list.

The *Bulletin of the Torrey Botanical Club* for January contains the following articles: Salmon, "Supplementary notes on the Erysiphaceæ"; Anderson, "*Dasyscypha resinaria* causing Canker Growth on *Abies balsamea* in Minnesota" (2 pls.); Anderson, "*Tilletia horrida* on Rice Plant in South Carolina"; and Rennert, "Seeds and Seedlings of *Arisæma triphyllum* and *A. dracontium*" (1 pl.).

A new edition of *Dörfles's Botaniker-Adressbuch* has recently been issued by the editor, and bears the imprint of Vienna.

The principal articles contained in the *Botanical Gazette* for January are the following: Harper, "Binucleate Cells in Certain Hymenomycetes" (1 pl.); Clark, "On the Toxic Properties of

¹ Huntington, Annie Oakes. *Studies of Trees in Winter*. Illustrated with colored plates and photographs. Boston, Knight Millet, 1902. xviii + 198 pp.

Some Copper Compounds with Special Reference to Bordeaux Mixture" (7 figs.); Clinton, "*Cladochytrium alismatis*" (3 pls.); Arthur, "Clues to Relationship among Heterœcious Plant Hosts"; Gooding, "Rocky Mountain Plant Studies, I."

The January number of *Country Life in America* is a California number. Among things of interest to the botanist are excellent habit photographs of *Washingtonia filifera*, *Sequoia gigantea*, *Quercus lobata*, *Yucca arborescens*, and the famous Monterey cypresses, and an exquisite flower portrait of *Romneya coulteri*.

In *Country Life in America* for February Mrs. Comstock writes on trees, Mr. Davy on the poppyworts, the editor on the nature-study idea, and Mr. Mowbray on the gardens of the old Hudson River manors. Many of the half-tone illustrations are not only exquisite but of botanical value.

The fifth fascicle of Vol. I of Mr. Howell's *Flora of Northwest America* reaches into the genus *Plantago*, the Benthamian sequence being followed. Like preceding parts, it contains descriptions of a few new species.

A phytogeographic paper on Silesia, by Schube, is published as a complementary Heft to Bd. LXXVIII of the *Jahresbericht der Schlesischen Gesellschaft für vaterländische Cultur*.

Vol. XVI of the *Acata societatis pro fauna et flora fennica* is entirely devoted to papers discussing the flora of the country.

In Vol. XIII of the *Verhandlungen der Naturforschenden Gesellschaft in Basel* Binz gives an interesting comparison of the present flora of that part of Switzerland in comparison with what Bauhin knew of it three centuries ago.

Vol. IV of Engler and Drude's *Vegetation der Erde* is by Beck von Mannagetta, and deals with the Illyrian region. It is published by Engelmann of Leipzig.

A historical bibliography of the flora of Rome is in course of publication by Pirota and Chiovenda, in the *Annuario* of the botanical institute of that city.

A second part of Ross' "Beiträge zur Flora von Sizilien" is published in No. 12 of the *Bulletin de l'Herbier Boissier* for 1901.

A paper on Dr. Baldacci's Albanian collections of 1897 has recently been separately printed from the *Memoire* of the Bologna Academy.

A list of new plants from the Cape Peninsula is published by Major Wolley Dod in the December number of the *Journal of Botany*.

An account of the vegetation of the Caroline Islands, by Volkens, is published in Bd. XXXI, Heft 3, of the *Botanische Jahrbücher*. Several interesting process plates accompany the text.

Several botanical papers are contained in the recently issued second part of Vol. XXVI of *Proceedings of the Linnæan Society of New South Wales*.

Vol. XXXIII of the *Transactions and Proceedings of the New Zealand Institute* contains the following botanical papers: Cockagne, "Seedling Forms of New Zealand Phanerogams," "Gunnera and Myosotis in Chatham Islands"; Laing, "Seaweeds of Norfolk Island"; Walsh, "*Cordyline terminalis* in New Zealand"; Cheeseman, "Cultivated Food Plants of the Polynesians, with Special Reference to *Cordyline terminalis*," "Recent Additions to the New Zealand Flora"; Thomson, "Plant-Acclimatisation in New Zealand"; Rutland, "Regrowth of the Totara"; Petrie, "Descriptions of New Native Plants"; Brown, "Notes on the New Zealand Musci." In the *Proceedings of the Affiliated Societies* some minor botanical notes are given, among them a rather curious surmise concerning *Selaginella lepidophylla*.

The announcement of the Marine Biological Laboratory at Woods Hole sets forth an attractive programme of studies and lectures for the coming summer. In the department of botany courses are provided in cryptogamic botany by Dr. Dacis, Dr. Moore, and Mr. A. C. Moore; in ecology by Dr. Cowles and Dr. Shaw; in plant physiology by Dr. R. H. True, and in cytology by Dr. Davis and Mr. Wolfe. In addition to the work of the session, which will extend from July 2 to August 13, an expedition will be organized to Mt. Katahdin and the coast of Maine for the purpose of conducting ecological studies in that region.

CORRESPONDENCE.

Editor of the American Naturalist:

SIR:—In a paper on "The Colors of Northern Polypetalous Flowers," in the March number of the *Naturalist*, p. 295, Mr. Lovell states that *Halictus nelumbonis* confines its visits to the flowers of *Nuphar* (*Nymphaea*) *advena*. In *Transactions of the American Entomological Society*, Vol. XVII, p. 316, 1890, it is recorded that this bee was taken on flowers of *Nuphar*, *Nymphaea*, and *Nelumbo* in Illinois, on *Nuphar* and *Nymphaea* in Florida, and on *Nuphar* in Wisconsin. It has been mentioned as a general visitor of *Nymphaeaceae* in *American Naturalist*, Vol. XXIX, p. 107; *Botanical Gazette*, Vol. XXVI, pp. 29, 36; *Illustrirte Zeitschrift für Entomologie*, Bd. V, p. 310; *Botanisches Centralblatt*, Bd. LXXXV, pp. 299, 302; *Botanischer Jahresbericht*, Bd. XXVII, Abth. 2, p. 463. No doubt the female gets pollen exclusively from flowers of *Nymphaeaceae*; but I have found her visiting for nectar the flowers of *Eriocaulon gnaphalodes*, *Utricularia inflata*, *Berlandiera subcaulis*, and *Verbena urticifolia*.

On page 235, in regard to the visitors of Umbelliferae, he says: "In Germany there have been collected on the caraway 55, on the wild carrot 61, and on the wild parsnip 118 insects. Probably the number of visitors to many species exceeds 200." The plant called wild parsnip by Mr. Lovell is *Heracleum spondylium*. In *Transactions of the Academy of Science of St. Louis*, Vol. V, p. 459, 1890; *Botanisches Centralblatt*, Bd. XLVI, p. 110; *Botanischer Jahresbericht*, Bd. XVIII, Abth. 1, p. 509, visitors are credited to several species as follows: *Zizia aurea*, 131; *Eryngium yuccifolium*, 147; *Tiedemannia rigida*, 156; *Heracleum lanatum*, 174; *Sium cicutifolium*, 191; *Cicuta maculata*, 238; *Pastinaca sativa*, 275.

In the literature the status of Müller's view regarding the influence of dull yellow colors on the visits of beetles is about as follows: The general proposition was refuted by Bonnier in 1879.¹ In the Tyrol, Schulz² not only found beetles on such flowers, but also distinctly stated that the general proposition was not true for that region.

¹ Les nectaires, *Ann. Sci. Nat. Bot.*, ser. vi, vol. 8, p. 71.

² Beiträge zur Kenntniss der Bestäubungseinrichtungen und Geschlechtsvertheilung bei den Pflanzen. Bd. ii (1890), p. 64.

In the same year I discussed the subject in connection with the Umbelliferae,¹ enumerating the visits of forty species of beetles to flowers of *Pastinaca*, which is nearly twice as many as Müller ever found on any umbellifer. In the *Botanical Gazette*, Vol. XXII, p. 169, 1896, I have cited the statements of Bonnier and Schulz. Finally, Knuth,² in a volume devoted to the general principles of anthoecology, abandons Müller's view with the statement that Müller himself and Loew had made observations which did not support it. He does not mention the observations of Bonnier, Schulz, or mine; but, of course, when a man feels at liberty to use the literature in any way he likes, he can record old things as new, and give credit in any way that suits his fancy. These references ought to be enough to dispose of a proposition which was never supported by a reasonable presumption.

CHARLES ROBERTSON.

CARLINVILLE, ILL., April 4, 1902.

¹ *Trans. Acad. Sci. St. Louis*, vol. v (1890), p. 454.

² *Handbuch der Blütenbiologie*, Bd. i (1898), p. 224.

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